

UNIVERSIDADE FEDERAL DO RIO GRANDE DO NORTE  
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ELIANA FARIA DE OLIVEIRA

FILOGEOGRAFIA DE *CNEMIDOPHORUS OCELLIFER*  
(SQUAMATA: TEIIDAE) NA CAATINGA

NATAL, RN

2014

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Tese apresentada ao programa de Pós-Graduação em Ecologia da Universidade Federal do Rio Grande do Norte, como parte das exigências para a obtenção do título de Doutor em Ecologia.

Orientador:

Dr. Gabriel Correa Costa

Co-orientadores:

Dr. Daniel O. Mesquita

Dr. Frank T. Burbrink

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“Fazer da interrupção um caminho novo.  
Fazer da queda um passo de dança,  
do medo uma escada,  
do sono uma ponte,  
da procura um encontro.”

Fernando Sabino

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## SÍNTESE

Nas últimas décadas, as ciências biológicas têm experimentado uma verdadeira revolução com o uso crescente de dados genéticos. O desenvolvimento acelerado de tecnologias para obtenção e análise de dados moleculares tem facilitado cada vez mais o acesso a esse tipo de informação (Hickerson *et al.* 2011; Fujita *et al.* 2012). Com isso, a genética tornou-se uma das principais ferramentas na investigação de questões relacionadas aos mais diversos campos das ciências naturais, tais como ecologia, taxonomia, conservação e evolução. Em tempos de crise da biodiversidade, o acesso à informação genética oferece uma valiosa oportunidade para o preenchimento de importantes lacunas do conhecimento relacionadas, por exemplo, à origem e diversificação da biodiversidade, identificação de espécies crípticas e compreensão dos padrões de distribuição da diversidade genética.

A eficácia dos dados genéticos depende do uso de marcadores multilocus (Dupuis *et al.* 2012) e do emprego do método coalescente que rastreie as divergentes histórias genealógicas até um ancestral comum (Fujita *et al.* 2012). Ao incorporar esses recentes avanços metodológicos, a filogeografia ampliou seu foco e tornou-se um dos campos mais integradores da biologia evolutiva (Hickerson *et al.* 2011). Além de identificar e delimitar áreas com histórias evolutivas singulares (Hickerson *et al.* 2011), o conhecimento filogeográfico também fornece *insights* valiosos sobre os modos de dispersão, extinções, expansão demográfica, áreas de refúgios, tempos de diversificação, bem como os padrões e processos responsáveis pela origem e manutenção da diversidade de espécies (Turchetto-Zolet *et al.* 2013).

As maiores lacunas de conhecimento filogeográfico mundial foram identificadas na América do Sul (Beheregaray 2008), onde os biomas xéricos foram reconhecidos como os menos conhecidos (Turchetto-Zolet *et al.* 2013). As Florestas Tropicais Sazonalmente Secas estão

distribuídas em várias manchas disjuntas na região Neotropical, sendo que a maior mancha, a mais isolada e diversa em espécies é o bioma da Caatinga, localizado no nordeste do Brasil (Werneck 2011; Werneck *et al.* 2011). Para entender como se deu a diversificação das espécies da Caatinga é necessário examinar as causas da estruturação filogeográfica em espécies com ampla ocorrência no bioma. O lagarto *Cnemidophorus ocellifer* é um dos mais comuns na Caatinga, e vários estudos sugerem que esta espécie corresponde, na verdade, a um conjunto de várias espécies crípticas (e.g. Arias *et al.* 2014; Harvey *et al.* 2012; Rocha *et al.* 1997; Rodrigues 2003). Assim, o complexo de espécies *C. ocellifer* apresenta uma oportunidade ideal para a investigação dos fatores históricos e ecológicos que influenciam a diversificação na Caatinga.

O primeiro capítulo desta tese teve como objetivo preencher parte da lacuna filogeográfica deste bioma, investigando através de uma abordagem genética integrativa os processos básicos que geraram a sua biodiversidade. A partir de uma amostragem multilocus e do emprego de métodos coalescentes, reconstruções filogeográficas e teste de modelos, foi possível reconhecer no complexo *C. ocellifer* duas espécies crípticas bem suportadas e associadas a duas regiões geográficas distintas da Caatinga. A espécie que corresponde propriamente a *C. ocellifer* ocorre em quase toda a Caatinga e áreas litorâneas adjacentes, enquanto a recém-descrita espécie *C. xacriaba* ocupa parte do Cerrado e o sudoeste da Caatinga. A divergência dessas espécies ocorreu durante o Mioceno na presença de fluxo gênico. A região centro-norte da Caatinga foi apontada como provável centro de origem de *C. ocellifer*, enquanto barreiras geográficas como a Serra do Espinhaço aparentemente impediram o contato secundário entre as espécies.

O reconhecimento de *C. ocellifer* como restrita à Caatinga e áreas litorâneas adjacentes oferece uma oportunidade de se investigar, pela primeira vez, como as características ambientais desse bioma influenciam os padrões espaciais de variação genética de sua biota. Diferentes aspectos da paisagem podem favorecer a conectividade espacial e aumentar as taxas de fluxo

gênico entre as populações (e.g. Lawson 2013). Por outro lado, algumas características do ambiente podem impor resistência ao fluxo gênico ou até mesmo agir como barreira, favorecendo a diferenciação genética de algumas populações (e.g. Ortego *et al.* 2012). Em um ambiente com condições extremas como a Caatinga, marcado por altas temperaturas e períodos de seca severa (Werneck 2011; Werneck *et al.* 2011), é interessante compreender de que maneira as características climáticas afetam a distribuição espacial da variação genética da sua biodiversidade. O papel das condições climáticas e de possíveis barreiras geográficas, como rios e complexos montanhosos, nos processos microevolutivos das espécies da Caatinga é ainda uma área pendente de investigação.

Neste contexto, o segundo capítulo da presente tese teve como objetivo principal testar a influência das características climáticas, do passado e do presente, bem como dos rios e do relevo da Caatinga, nos padrões espaciais atuais da variação genética em *C. ocellifer*. Através da modelagem de nicho ecológico e da teoria de circuito, foi possível verificar que a variação genética em *C. ocellifer* é influenciada pela variabilidade da temperatura, que parece modular as taxas de fluxo gênico entre as populações. Condições ambientais do passado foram importantes na formação da diversidade genética atual, sugerindo um atraso na resposta genética. Padrões de diferenciação genética em *C. ocellifer* foram explicados tanto por isolamento pela distância quanto pelo isolamento por resistência. Neste último caso, diferenças na adequabilidade do nicho e a resistência imposta pelos principais rios foram preponderantes para gerar o padrão atual observado.

Os resultados aqui apresentados adicionam novas informações à compreensão dos processos envolvidos na origem e manutenção da diversidade na Caatinga, nas escalas macro e microevolutiva. Além de contribuir com a resolução taxonômica do complexo *C. ocellifer* através do reconhecimento de duas unidades evolutivas independentes, este estudo identificou os

principais aspectos da paisagem da Caatinga que moldaram a distribuição da sua variação genética. As informações aqui geradas, sobretudo relacionadas à distribuição da diversidade genética, poderão fundamentar futuras estratégias de conservação de *C. ocellifer*.

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# CAPÍTULO I

Speciation with gene flow in whiptail lizards from a Neotropical xeric biome

## Speciation with gene flow in whiptail lizards from a Neotropical xeric biome

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## **Abstract**

Quantifying biodiversity and revealing the historical processes involved in the processes of speciation are fundamental for understanding why particular biomes are so diverse.

Phylogeographic inference can provide essential information relating to the timing of population divergence, historical demography, and patterns of migration revealing processes responsible for the origin and maintenance of biodiversity. One of the most complex biomes in South America, the Caatinga is part of a wide area of Seasonally Dry Tropical Forests, yet understanding how diversity in this region accrues is largely unknown. We employed an integrative approach using multilocus data and phylogeographic reconstructions to understand regional impacts on population structure of the *Cnemidophorus ocellifer* species complex from the Caatinga. Using coalescent methods, we found two well-supported cryptic species in the Caatinga associated to two different geographic regions. Species divergence occurred during the mid-late Miocene (*c.* 10.5 Ma) and the model-based analysis suggests parapatric speciation with gene flow along environmental gradients. The central-northern Caatinga region served as an important center of origin, harboring more ancient lineages. Our findings highlight the possible role of the Cerrado biota contributing to the Caatinga diversity.

*Keywords:* ABC approach, Caatinga biome, *Cnemidophorus*, coalescent methods, Miocene diversification, phylogeography

## Introduction

Knowing how many species there are on Earth and understanding the processes that lead to the origin of biodiversity are among the most fundamental questions in biology. Nearly 1.5 million eukaryotic species have been catalogued globally, although recent estimates indicate that over 85% of Earth's biota is still unknown (Mora *et al.* 2011; Costello *et al.* 2013). The Neotropical region is one the most diverse in the world (Rull 2008, 2011, 2013) and thousands of species were described during the past decade alone (Costello *et al.* 2013). Along with the general lack of information on the total Neotropical biodiversity, the historical processes involved in generating species, such as the relative roles of Neogene geomorphological events and Quaternary climatic fluctuations in biotic diversification (Turchetto-Zolet *et al.* 2013; Smith *et al.* 2014), are still hotly debated (Rull 2008, 2011, 2013). Empirical evidence to support this debate is still inconclusive (Rull 2013) and for many taxonomic groups and biomes, data is still nonexistent (Beheregaray 2008; Turchetto-Zolet *et al.* 2013).

Phylogeographic studies allow testing specific hypotheses related to the processes of diversification (Beheregaray 2008; Carnaval *et al.* 2009; Hickerson *et al.* 2010; Turchetto-Zolet *et al.* 2013). Some well-developed regional study systems have identified temporally and spatially clustered modes of speciation by comparing historical patterns of gene flow and divergence among co-distributed organisms (Hickerson *et al.* 2010), often driven by shared phylogeographic breaks at rivers, mountain chains, or Pleistocene refugia (e.g. Schönswetter *et al.* 2005; Swenson & Howard 2005; Soltis *et al.* 2006). Although documented as the most biodiverse continent, phylogeographic studies in South America are lacking relative to the temperate regions of the world (Beheregaray 2008). In the last decade, however, phylogeographic research has accelerated throughout the continent and revealed emerging patterns, including a recent origin of many South American species during the mid-

Pleistocene and signals of restricted distributions of species associated with forest habitats during glacial cycles (Turchetto-Zolet *et al.* 2013).

In particular, how biodiversity is generated, especially in the open vegetation biomes of South America, remains an open question for most organisms (Werneck 2011; Turchetto-Zolet *et al.* 2013). For example, little is known about diversification processes in Seasonally Dry Tropical Forests (hereafter SDTF), which form numerous disjunct patches in the Neotropical region (Werneck 2011). The Caatinga biome in northeastern Brazil represents the largest, most isolated and species-rich SDTF (Werneck 2011), with high levels of diversity and endemism reported for several groups (e.g. Rodrigues 1996, 2003; Zanella & Martins 2003; Queiroz 2006). Semiarid vegetation, high temperatures, and a severe dry season characterize the Caatinga. However, turnover in habitat types in this region was likely common in the past and wetter climate and humid vegetation has been inferred for the Caatinga during the late Pleistocene and early Holocene (De Oliveira *et al.* 1999; Behling *et al.* 2000; Auler *et al.* 2004; Wang *et al.* 2004). Conversely, disjunct distributions of squamate species in isolated sandy soil patches suggest a past climate similar or even drier than current conditions, when these sandy areas were putatively more extensive and continuous (Rodrigues 1996, 2003). Investigating the historical demography of endemic species can provide new insights about the role of that environmental stability or climatic fluctuation on diversification of the Caatinga biota.

General historical processes affecting the origin and distribution of the Caatinga biodiversity are still poorly known (Werneck 2011; Werneck *et al.* 2011), though some hypotheses have been proposed. The longest perennial river in the Caatinga, the São Francisco River (hereafter SFR), has been considered a potential barrier to gene flow for several animal taxa. The geographic distribution and phylogenetic relationships of some groups suggest frequent past connections between both banks of the SFR, such as tropidurid

lizards (Passoni *et al.* 2008), eyelid-less lizards (Siedschlag *et al.* 2010), and rodents (Nascimento *et al.* 2011; Nascimento *et al.* 2013). Conversely, other taxa exhibit unique phylogeographic patterns. For example, the Caatinga lineages of the gecko *Phyllopezus* diverged along environmental gradients, while the SFR likely prevented secondary contact between lineages, reinforcing its importance as a singular biogeographic barrier (Werneck *et al.* 2012). Generally, widespread lineages in the Caatinga, including plants (Caetano *et al.* 2008), geckos (Werneck *et al.* 2012), frogs (São Pedro unpublished data), and gymnophthalmid lizards (Recoder *et al.* 2014), show reduced phylogeographic structure, likely related to the few geological barriers that would hamper gene flow or because of recent dispersals to the region.

To further understand how changing environments and putative barriers affect species diversification in the Caatinga, it is necessary to examine the phylogeographic structure of widespread species across this region and infer the processes shaping the current patterns of genetic variation. The whiptail *Cnemidophorus ocellifer* (Spix 1825) is one of the most common lizards in the Caatinga and several studies have suggested that it comprises multiple cryptic species (e.g. Rocha *et al.* 1997; Rodrigues 2003). Hence, the *C. ocellifer* species complex presents an opportunity to investigate the historical and ecological factors that influence diversification in Caatinga. Our study attempts to fill a gap in the basic knowledge of diversity generated at young time scales in the Caatinga using an integrative genetic-modeling approach. We obtained a range-wide sampling of this species for multiple loci to infer population structure, biogeographic barriers, and historical demography. Our results yield new insights about the drivers of diversity in a poorly known, yet diverse biome in South America.

## Materials and Methods

### *Sample collection and sequencing*

We obtained 398 tissue samples of the *Cnemidophorus ocellifer* species complex (see ‘Taxonomic Background’, Supporting information) from 78 localities in the Caatinga biome and adjacent areas (Fig. 1 and Table S1, Supporting information). Samples were obtained through fieldwork led by the authors and through loans from different herpetological collections. *Cnemidophorus venetacaudus*, a member of *C. ocellifer* group (or *C. littoralis* subgroup; see ‘Taxonomic Background’, Supporting information), was used as outgroup when necessary.

We extracted DNA from liver or muscle tissue using Qiagen DNeasy kits. Five loci were amplified via polymerase chain reaction (PCR) using GoTaq Green MasterMix (Promega Corporation). Details about loci, primers, and PCR protocols are listed in Table S2 (Supporting information). We cleaned PCR products with 2 µl of ExoSap (USB Corporation) and sequenced the products using 1 µl of each primer, 2 µl of DTCS (Beckman-Coulter), and 4 µl of ultrapure water. First, we sequenced all individuals for one mitochondrial DNA (mtDNA) gene (12S ribosomal RNA; 12S). For nuclear (nuDNA) genes, we sequenced a subset of individuals (137 samples), which were chosen to represent a wide geographic range within the Caatinga (i.e. the same 78 collecting localities). We sequenced four nuDNA genes: ATP synthase beta subunit (ATPSB), natural killer-tumor recognition sequence (NKTR), G protein-coupled receptor 149 (R35), and ribosomal protein 40 (RP40). All sequences were generated using Sanger sequencing, aligned with the Clustal algorithm (Sievers *et al.* 2011), and checked by eye using Geneious 6.1 (Biomatters). We found gaps in 12S and ATPSB genes and removed them using Gblocks (Castresana 2000; Talavera & Castresana 2007), available as a web server ([http://molevol.cmima.csic.es/castresana/Gblocks\\_server.html](http://molevol.cmima.csic.es/castresana/Gblocks_server.html)). This program reduces the need for manually editing multiple alignments, making the automation of



phylogenetic analysis of large data sets feasible; it also facilitates the reproduction of the alignments and subsequent phylogenetic analysis by other researchers. To determine the most probable pair of alleles for each nuDNA gene, we used the PHASE algorithm (Stephens *et al.* 2001) implemented in the DnaSP 5.10 software (Librado & Rozas 2009). Only samples with probability of pairs of alleles in heterozygosity higher than 80% were considered in the following analyses. All sequences obtained in this study are available at GenBank (access numbers available after acceptance for publication).

#### *Population structure and assignment*

We used two approaches to investigate population structure in *C. ocellifer*, both using a statistical model based on Bayesian inference to infer groups and assign individuals to these groups. First, we used a genotype matrix (see Falush *et al.* 2003) of the four nuDNA genes to investigate population structure with STRUCTURE 2.3.4 (Pritchard *et al.* 2000). We explored a large range of values by running 10 replicate analyses over a range of number of populations ( $k$ ) from 1 to 10. Each independent run implemented  $5 \times 10^4$  generations following a burn-in of  $5 \times 10^4$  generations, assuming a linkage model and uncorrelated allele frequencies. We chose the best value of  $k$  based on the rate of changes in the log-probability of data between successive  $k$  values,  $\Delta k$  (Evanno *et al.* 2005), using Structure Harvester (Earl & vonHoldt 2012). Second, we ran GENELAND 4.0.3 (Guillot *et al.* 2005a; Guillot *et al.* 2005b) implemented in R (R Development Core Team 2015), which uses a clustering algorithm of STRUCTURE under a spatial model. This analysis evaluates the presence of population structure in a group of geo-referenced genotypic or haplotypic data by inferring and identifying genetic discontinuities. We used two different haplotype data sets, one with just nuDNA data and another with both mtDNA and nuDNA data. The most probable number

of population units ( $k$ ) was determined by a Markov Chain Monte Carlo (MCMC) method, with 10 repetitions ( $5 \times 10^6$  iterations in each) of  $k$  from 1 to 10.

#### *Genetic diversity and genetic distances*

For each population identified by STRUCTURE and GENELAND (both programs generated identical results), we calculated the number of polymorphic sites ( $S$ ), haplotype number ( $h$ ), haplotype diversity ( $Hd$ ), nucleotide diversity ( $\pi$ ), Tajima's  $D$  and its  $P$  value for each locus using DnaSP. We investigated genetic structure between and within populations and loci with analyses of molecular variance (AMOVA) in Arlequin 3.5 (Excoffier & Lischer 2010), using 10,000 permutations. We also estimated uncorrected pairwise genetic distances between and within populations identified for all genes in MEGA 6.06 (Tamura *et al.* 2013) using default options.

#### *Gene tree estimation and haplotype genealogy*

We estimated gene trees independently for mtDNA and nuDNA (unphased) genes using Bayesian inference in BEAST 1.8 (Drummond *et al.* 2012). We determined the most appropriate substitution model using Bayesian Information Criterion (BIC) in jModeltest (Posada 2008; see Table S3, Supporting information). We ran  $2 \times 10^7$  generations sampled every  $2 \times 10^3$  generations, resulting in five gene trees. We visually assessed convergence of the MCMC runs and effective sample sizes (ESS values  $\geq 200$ ) using TRACER 1.6 (Drummond & Rambaut 2007). The first two thousand generations were discarded as burn-in and the consensus tree for each locus was inferred with TreeAnnotator 1.8 (Drummond *et al.* 2012). Table S3 (Supporting information) shows other details of these analyses.

We estimated haplotype networks for mtDNA and nuDNA (phased) genes using the median joining (MJ) method (Bandelt *et al.* 1999) in NETWORK 4.6.1.2 ([www.fluxus-](http://www.fluxus-)

engineering.com). However, MJ networks recovered many unresolved loops in the genealogical connections between haplotypes (Fig. S1, Supporting information). Following Sequeira *et al.* (2011), we used phylogenetic algorithms to generate haplotypes networks. We then used a maximum likelihood (ML) approach with PHYML 3.1 (Guindon *et al.* 2010), using default options and the best-fit model for each locus (Table S3, Supporting information). We used ML trees to estimate each network haplotype in Haploviewer (Salzburger *et al.* 2011).

### *Species tree estimation*

We estimated a species tree and provided a reliable divergence date among putative species. To calibrate the species tree, we used a 12S substitution rate derived from a calibrated gene tree using a Bayesian phylogenetic method. First, we downloaded teiid sequences from GenBank (one outgroup and other 59 sequences) and added two *C. ocellifer* sequences from this study (Table S4, Supporting information). We then ran a 12S gene tree applying four node constraints based on appropriate fossil evidence (see ‘Fossil Record’, Supporting information): (i) origin of Teiidae at 56 Ma; (ii) divergence of *Tupinambis* from other Tupinambinae at 21 Ma; (iii) origin of “cnemidophorine” at 20.4 Ma; and (iv) divergence of *Dracaena* from other Tupinambinae at 13.8 Ma. Based on the most recent phylogeny of Squamata (i.e. Pyron *et al.* 2013), we enforced the monophyly of each clade used in the calibration scheme. Because “cnemidophorine” is not monophyletic (see Pyron *et al.* 2013), we used the “cnemidophorine” fossil to place a minimum constraint at the origin of Teiinae. We then enforced time constraints using lognormal distributions, so that fossil ages would represent the youngest limit for the respective node divergence without defining a hard limit for older divergences. Accordingly, the resulting 5%-95% prior distributions were: 56 to 71.4 Ma (Teiidae), 21 to 40.8 Ma (*Tupinambis*), 20.4 to 40.25 Ma (Teiinae), and 13.8 to 35.1 Ma

(*Dracaena*). We used an uncorrelated lognormal relaxed clock with a Yule speciation-process prior and ran BEAST for  $1 \times 10^8$  generations, sampled every  $1 \times 10^4$  generations. From this analysis, we obtained a 12S substitution rate of  $5.11 \times 10^{-3}$  (equivalent to  $5.11 \times 10^{-9}$  substitutions/site/year), which is similar to mtDNA rates found in other squamates groups (Eo & DeWoody 2010). We used this estimated rate as a fixed parameter for the 12S substitution rate in the species tree estimation.

We estimated a *C. ocellifer* species tree using \*BEAST 1.8 (Drummond *et al.* 2012). Coalescent-based species tree tracks the divergent genealogical histories back to a common ancestor through an objective and comparable method (Fujita *et al.* 2012). \*BEAST simultaneously estimates the relationship between species, divergence times, and population size of each species. \*BEAST requires *a priori* assignment of individual alleles to a species before estimating the relationship and we therefore made assignments based on STRUCTURE and GENELAND results (both generated identical results). This analysis was run for  $5 \times 10^8$  generations and sampled every  $5 \times 10^4$  generations (more details in Table S3, Supporting information). The first 20% of sampled genealogies were discarded as burn-in and the most credible clade was inferred with TreeAnnotator.

### *Historical demography*

We generated Bayesian Skyline Plots (Drummond *et al.* 2005) in BEAST to estimate past population dynamics through time for each delimited taxa, using only the mtDNA data. We attempted to run multilocus Extended Bayesian Skyline Plot (Heled & Drummond 2008) in BEAST, but the MCMC failed to reach stationarity. To calibrate the molecular clock, we used a mtDNA substitution rate of  $5.11 \times 10^{-9}$  substitutions/site/year. We ran three independent chains of  $5 \times 10^7$  generations sampling every  $5 \times 10^3$  generation (more details in Table S3, Supporting information). Parameter convergence, stationarity, and effective sample sizes were

visually assessed using TRACER, and the graphs of population dynamics through time were generated in the same program.

### *Migration*

We used the coalescent-based program IMA2 (Hey & Nielsen 2007; Hey 2010) to estimate gene flow, ancestral and current population sizes, and divergence time between species. We used all loci in this analysis. We provided estimates of mutation rates (substitutions/locus/year) based on estimates from the species tree for each gene. We applied the HKY model (Hasegawa *et al.* 1985) for all genes and an inheritance scalar of 0.25 and 1.0 for mtDNA and the four nuclear loci, respectively. We used a generation time of 2 years, which was estimated for other teiid lizards [*Aspidoscelis tigris* (Dessauer *et al.* 2000) and *Ameiva chrysoleama* (Gifford & Larson 2008)]. Upper prior limits for population parameters were defined following the IMA2 manual ( $q = 22.45$ ,  $t = 8.98$ ,  $m = 0.45$ ). First, we conducted a short preliminary run to check convergence of parameters with 20 chains and the geometric heating model as suggested by the manual. We then performed an M-mode run using ‘IMburn’ file to inspect the trend plots to ensure stationarity and control the length of the burn-in ( $> 1,800,000$  steps). The recording phase had  $1 \times 10^7$  steps sampling genealogies every 100 step. Finally, we conducted an L-mode run using 100,000 sampled genealogies to test a total of 25-nested models. We used log-likelihood ratio tests to compare these nested models and AIC to discriminate between models not rejected by the tests.

### *Phylogeographic reconstructions*

We used four nuDNA (phased) and the mtDNA genes to reconstruct the spatial distribution and occupancy of areas by *C. ocellifer* through time. First, we tested both lognormal relaxed random walk (RRW) and Homogenous Brownian models (Lemey *et al.* 2010) implemented in

BEAST. Because *uclid.stdev* values (visualized in TRACER) of the lognormal RRW model did not suggest distinct dispersal rates for different branches (posterior distribution included zero), we generated all phylogeographic reconstructions from Homogenous Brownian model. Substitution rates of nuclear loci were obtained from the species tree estimation (see values in Table S3, Supporting information). We used a jitter option of 0.05 because some samples coordinates (used as a trait) were duplicated. Some parameter values used in BEAST, as MCMC and sampled steps were set differently according to each gene to reach convergence checked by TRACER. The first 20% of sampled genealogies were discarded as burn-in and the maximum clade credibility tree was computed with TreeAnnotator. These trees were used as input for the program SPREAD 1.0.4 (Bielejec *et al.* 2011) to generate a keyhole markup language file (.kml) containing the phylogeographic history. We visualized kml files in Google Earth. The feasible center of origin was considered by overlapping the center of origin for all genes.

#### *Tests of diversification scenarios*

We used an Approximate Bayesian Computation (ABC) approach (Beaumont 2010) to test alternative biogeographic scenarios for the diversification of the *C. ocellifer* lineages. ABC is a simulation-based method assuming different parameter and prior values under competing models (Csilléry *et al.* 2010). Analyses consisted of three steps: (i) sample parameter values from the prior distributions to simulate data under each model; (ii) compute summary statistics of the simulated datasets; and (iii) compare simulated to observed data using ABC rejection/regression algorithms to estimate the probability of simulated models.

We simulated four diversification scenarios: (A) *Divergence with gene flow*. This model is equivalent to the IMa2 model, which does not incorporate population size changes. By including it, we test whether a simple scenario with less parameters could explain our results.

(B) *Divergence with gene flow and recent population expansion in both lineages*. BSP analyses and/or Tajima's D tests show signatures of population expansion for both lineages (see Results). (C) *Divergence with gene flow and recent population expansion in Northeast lineage*. Because population expansion is significant only for Northeast lineage (see Results), we also considered a model with a single expansion as possibility. (D) *Divergence with gene flow and founder effect for the Northeast lineage*. The phylogeographic reconstruction supports the geographical origin of the Northeast lineage close to the contact zone and the BSP shows a strong increase in its population size (see Results), which may suggest a founder effect with range expansion. Taking into account these four scenarios, we then compared the four models representing variations within each scenario. We assumed two different divergence times ( $T_1$ ) for each scenario based on \*BEAST and IMa2 results (see Results). We also considered two possibilities of migration histories: one with migration throughout the population history and another with recent migration (i.e. a possible secondary contact;  $T_2$ ). All combinations resulted in 16 tested models (i.e. four models for each scenario).

We performed 1,000,000 simulations for each model using msABC (Pavlidis *et al.* 2010). Because msABC does not implement priors for mutation rates, we used an R script to sample parameters from prior distributions and call msABC. Parameter prior distributions were based on results of \*BEAST, Bayesian Skyline Plot (BSP), and IMa2 analyses (see Results and Table S5, Supporting information). We implemented priors in demographic quantities and transformed to *ms* scaled parameters using equations from the *ms* manual (Hudson 2002). We called msABC one time for each gene (i.e. five genes) using the same number of samples and length of loci. For the mitochondrial gene, we used ¼ of the sampled population size. Five summary statistics for each gene were used: nucleotide diversity and Tajima's D for each population, and the  $F_{ST}$  between populations. We transformed observed sequence data into ms-like files using a *fas2ms* perl script (from msABC package) and

calculated the same summary statistics for each locus. To estimate posterior probabilities and model support ('postpr' function), we used R package 'abc' (Csilléry *et al.* 2012). We first compared the four possibilities within each scenario and kept the most probable one for a comparison among scenarios. We set tolerance to 0.0001 and implemented both the multinomial logistic regression and nonlinear neural network regression methods. Because ABC could not attain resolution in comparison among scenarios, we increased the tolerance rate to 0.001. We summarized simulated model fit to the observed data using a Principal Components Analysis (PCA) calculated in R.

## Results

### *DNA polymorphism, population structure and species tree estimation*

We sequenced all 398 individuals for mtDNA 12S gene (Table S1, Supporting information) and a subset of 137 individuals for nuDNA (Table S6, Supporting information). The nuDNA loci resulted in 115-134 sequences for each gene (Table 1). Only ~ 7% of the data was missing for all nuDNA loci. ATPSB and 12S sequences preserved ~ 89% (623 bp) and ~ 94% (370 bp) of their original size, respectively, after gap exclusion by Gblocks. The number of variable sites was highest in 12S (96 sites), with a maximum of 56 (ATPSB) and a minimum of 15 (RP40) for nuDNA loci. Table 1 shows additional information for all genes and population genetic statistics for each locus and each *C. ocellifer* lineage.

Using a genotype matrix, STRUCTURE detected two populations ( $k = 2$ ; see Fig. S2, Supporting information). An identical result, with the same individuals being assigned to each population, was obtained using the haplotype dataset in GENELAND (Fig. 2). These populations are associated with two distinct geographic regions. One is distributed from north to southeastern Caatinga, occupying a large part of this biome (hereafter Northeast lineage). The second occurs southwest of the Caatinga (i.e. Espinhaço Mountain Range, hereafter



EMR) and adjacent areas of Cerrado biome (hereafter Southwest lineage). According to Bayesian gene trees (Fig. S3, Supporting information), the Northeast lineage presents shallower subclades than those of the Southwest lineage. Most individuals are grouped in exclusive subclades of each lineage, although Northeast and Southwest lineages are not reciprocally monophyletic and show some admixture. However, population structure can be easily visualized through mtDNA and nuDNA haplotype genealogies, and few haplotypes are shared between Northeast and Southwest lineages in all genes (Fig. 3). The Southwest lineage presents higher haplotype and nucleotide diversity than the Northeast lineage (Table 1).

AMOVA showed high values of  $F_{ST}$  (28-66%) for all genes. In three genes (ATPSB, NKTR, and RP40) the source of genetic variation was greater between lineages (Table 2). Uncorrected mtDNA p-distances exhibited substantial genetic differences (3.6%) between Northeast and Southwest lineages (Table 3). \*BEAST analyses showed that the Northeast and Southwest lineages diverged around 2.07 Ma (95% HPD = 1.18 to 3.10 Ma), during the early Pleistocene.

#### *Historical demography and migration*

BSP showed that the Southwest lineage experienced no population size change according to the confidence interval, whereas the Northeast lineage revealed a dramatic increase in population size through time, with accelerated growth during the late Pleistocene (Fig. 4).

From the IMA2 analyses, we detected that the likelihood ratio tests failed to reject three models in favor of the fully parametrized IM model (Table S7, Supporting information). AIC could not easily discriminate between two models given their low  $\Delta AIC$  values. Both models have equal migration in both directions; one model suggests that extant population sizes are equal but both are different from the ancestral population size, and the other model assumes distinct population sizes (Table S7, Supporting information). Equal migration in both

directions was inferred at 0.46 migrants per generation per gene copy (95% HPD = 0.17 to 0.77). Effective population sizes of Northeast and Southwest lineages were estimated to be much larger (at least six times) than the ancestral population (Table S8, Supporting information). Divergence between Northeast and Southwest lineages was dated at 10.55 Ma (95% HPD = 6.79 to 14.76 Ma), during the mid-late Miocene, which is not consistent with estimates from the species tree. Because we detected significant migration rates between Northeast and Southwest lineages, which violates \*BEAST assumptions, we considered the divergence time estimated by IMA2. However, some violations of the “Isolation and Migration” (IM) model can also affect parameters estimated by IMA2 (see Strasburg & Rieseberg 2010). For instance, gene flow from an unsampled species (i.e. third population) appears to have some upward bias in divergence-time estimates, even for moderate levels of gene flow (Strasburg & Rieseberg 2010). Considering that our sampling covers only the Caatinga and adjacent areas, and *C. ocellifer* species complex also reaches the entire Cerrado biome, this violation is possible. To address divergence inconsistencies, we simulated different divergence times in the model-based analysis (see results below).

### *Phylogeographic reconstructions*

Phylogeographic analyses suggest that the Northeast lineage originated in central-north Caatinga, encompassing a region in southeastern Piauí, southern Ceará, western Pernambuco, and northern Bahia states (Fig. 5). All genes independently indicated this same region as a feasible area of origin, but some genes revealed wider areas. The ancestral population subsequently expanded towards the north, east and south in Caatinga, and colonized the entire biome during the late Pleistocene (Fig. 5). Phylogeographic reconstructions were not conducted for the Southwest lineage because our sampling does not encompass sufficient geographical information (see Discussion) to get reliable results (Lemey *et al.* 2010).

### *Tests of diversification scenarios*

We modeled four alternative biogeographic scenarios for the diversification of *C. ocellifer* lineages (Fig. 6). First, we compared the four possibilities within each scenario and kept the most probable one for a comparison among scenarios. This comparison within each scenario favored the IMA2 divergence time for scenarios A, C, and D, whereas each regression method favored a different divergence for scenario B (Table 4). The same comparison also favored the constant migration for scenarios B, C, and D, whereas a recent migration was more probable for scenario A. Among the selected scenarios, ABC favored scenario D with IMA2 divergence and constant migration ( $P = 0.999$  or  $P = 1$ ; see Table 4). The observed summary statistics occurred within the bounds of the simulated summary statistics at PCA predictive plots, confirming good model fitting (Fig. S4, Supporting information).

### **Discussion**

We reveal clear genetic structure, cryptic genetic diversity that has its origin in the mid-late Miocene. Ultimately, our study represents one of the best-grounded examples of the Caatinga diversification histories by providing phylogeographic insights across the largest and most isolated SDTF nucleus.

### *Environmental changes and diversification*

The *Cnemidophorus ocellifer* species complex is structured into two distinct genetic lineages in the Caatinga. Our model-based analysis supports a diversification process with gene flow in which part of the Southwest lineage gave rise to the Northeast lineage (Table 4 and Fig. 6). This founder population subsequently expanded and colonized the entire Caatinga biome as supported by the phylogeographic reconstruction (Fig. 5). Although our model represents a

simplistic scenario for diversification history of these lineages, it suggests the prevalence of parapatric speciation process, implying that Southwest lineage has an older history than Northeast lineage. The model also supports an old divergence time, during mid-late Miocene, confirming the IMa2 results and rejecting the \*BEAST estimate. Because the \*BEAST coalescent model does not incorporate a migration parameter, the incomplete lineage sorting is translated into recent divergence. When accounting for migration, the incomplete lineage sorting can still be in agreement with an older divergence, as found by IMa2.

Speciation with gene flow is likely to represent ecological speciation through an environmental gradient (Nosil 2008). The divergence between Southwest and Northeast lineages coincides with the origin of some SDTF endemic plants that took place mostly during the mid-Miocene to Pliocene (Pennington *et al.* 2004). The intensification of Northern Hemisphere glaciation between the Late Miocene and the Late Pliocene may also have contributed with the expansion of semiarid climate in northeast Brazil (Werneck *et al.* 2015), and consequently the SDTF diffusion. Probably, a population located along the edge of the Southwest lineage distribution may have adapted to this new emerging niche, eventually evolving into the Northeast lineage and expanding with the SDTF. Alternatively, the Southwest lineage occurs in higher elevations (i.e. Cerrado biome and EMR) than the Northeast lineage (see Fig. 2). This altitudinal difference is part of an environmental gradient that may have driven ecological speciation. The putative geographic origin of the Northeast lineage near the northern boundary of the EMR (Figs 2 and 5) supports this assumption. Subsequently, EMR may also have acted as an ecological barrier preventing the contact between Southwest and Northeast lineages, because the latter colonized only adjacent lowland areas of the north and east side of the EMR (Fig. 5). Speciation with gene flow along environmental gradients has also been proposed to explain diversification between Caatinga and Cerrado lineages in the gecko *Phyllopezus pollicaris* (Werneck *et al.* 2012).

The SFR may have also played an important role in the Caatinga diversification, with some endemic genera and species pairs isolated on opposite riverbanks (Rodrigues 1996, 2003). Although the SFR originated in the Cretaceous (Potter 1997), its course and water volume were modified by inland tectonic activities and climate changes (Mabesoone 1994). Divergence estimates in lizards and rodents suggest the existence of past connections between SFR riverbanks and highlight the role of the SFR as a vicariant barrier during the Miocene and Pleistocene (*Eurolophosaurus*, Passoni *et al.* 2008; *Calyptommatius*, Siedschlag *et al.* 2010; *Calomys*, Nascimento *et al.* 2011; *Thrichomys*, Nascimento *et al.* 2013). During the Miocene, the SFR likely ran northward to the equatorial Atlantic Ocean (Mabesoone 1994; see also Nascimento *et al.* 2013; Werneck *et al.* 2015). Interestingly, the paleo-course of the SFR (Fig. 2, arrow b) was situated at the western limit of the geographic origin of the Northeast lineage. Part of the Southwest lineage may have colonized the other side of the paleo-river during the formation of temporary sand bridge and/or the change in watercourse, hence founding the ancient Northeast lineage. These temporary connections would allow some exchange of genes between the two lineages, and in the absence of bridges, the river would work as a barrier leading to diversification. Subsequently, Southwest lineage also colonized the other side of the SFR (Fig. 2, arrow a), but remaining restricted to high elevation areas (i.e. EMR). The ancient course of the SFR has played important role in the rodents diversification (Nascimento *et al.* 2013).

The two diversification mechanisms presented above (i.e. environmental gradient or SFR paleo-course) are non-mutually exclusive and both processes may have happened simultaneously. In this case, the paleo-river could act as a permeable barrier, restricting gene flow and accelerating the diversification while the founder population adapted to a new environment. Nevertheless, the existence of frequent temporary connections between SFR riverbanks is merely speculative, which weakens the riverine hypothesis. Therefore, we

consider that speciation with gene flow along environmental gradients is a more realistic mechanism for *C. ocellifer* diversification in Caatinga.

The apparent more recent origin of the Northeast lineage than the Southwest may be linked with Cerrado and Caatinga histories. According to a conservative view, Cerrado is of Eocene origin (see review in Werneck 2011), whereas SDF is younger, from the mid-late Miocene (Pennington *et al.* 2004). Recent studies have also identified a mid-late Miocene origin for the main Caatinga lineages (e.g. Werneck *et al.* 2012; Nascimento *et al.* 2013; Magalhães *et al.* 2014; São Pedro unpublished data), although latter origins have also been found (e.g. Nascimento *et al.* 2011; Nascimento *et al.* 2013; Machado *et al.* 2014; Werneck *et al.* 2015). Interestingly, some Caatinga lineages have showed recent population expansion (e.g. Werneck *et al.* 2015), or present short coalescent times (e.g. lineage VIII in Werneck *et al.* 2012) and short branch lengths (e.g. Recoder *et al.* 2014; São Pedro unpublished data), which are also consistent with a signal of population expansion. We suggest that signatures of population expansion may be a common pattern in Caatinga biota. It is possible that this pattern is coupled to the SDF expansion and, hence, the biota and the biome have expanded together. Other non-exclusive possibility is that this pattern is related to founder effect process with range expansion, as found in Southwest and Northeast lineages. We consider it may be a common speciation process in Caatinga biome. Thus, the Cerrado biota would be the major source of diversity for the formation of Caatinga biota. Although other diversification mechanisms may also occur, one way to investigate the Cerrado origin contribution is performing model-based tests for other groups distributed along both biomes.

Independent lines of evidence support that the Caatinga domain was wetter in distinct regions and periods during the last 210,000 years, favoring the expansion of humid forest (De Oliveira *et al.* 1999; Behling *et al.* 2000; Auler *et al.* 2004; Wang *et al.* 2004). Current natural rainforest enclaves (regionally called *brejos de altitude*) are likely remnants of these ancient

forests. Thus, part of the biota found today in the Caatinga region may have also originated from rainforest biotas and would have a more recent origin. Nevertheless, those species are not adapted to the xeric Caatinga and are currently restricted to highland humid areas.

#### *Phylogeographic implications*

*Cnemidophorus ocellifer* species complex shows clear genetic structure associated with two distinct geographic regions. Because this species complex also occurs in the entire Cerrado, we hypothesize that the Southwest lineage is part of a more widespread lineage from central Brazil that reaches southwestern Caatinga. Therefore, additional samples from central Cerrado are necessary to better define genealogic relationships within the Southwest lineage and its geographic boundaries. Even considering that the Southwest lineage may not be appropriately sampled, it showed higher genetic diversity than the Northeast lineage (Table 1). Part of the Southwest lineage samples comes from the Cerrado, a biome characterized by geomorphological complexity and elevated landscape heterogeneity at local and regional scales (Cole 1986; Fig. 2). Other samples are from high elevation areas associated with the EMR (Fig. 2, arrow c) that also present high habitat heterogeneity (Queiroz 2006). In general, spatial heterogeneity potentially enhances environmental opportunity for ecological divergence, consequently increasing genetic diversity (Werneck 2011). The EMR is well known for its high levels of endemism, including plants (Queiroz 2006), squamates (Cassimiro & Rodrigues 2009), and anurans (Leite *et al.* 2008). Moreover, our hypotheses testing support a relatively stable population size for the Southwest lineage (Table 4 and Fig. 6), which is in line with higher nucleotide diversity. Apparently, the Northeast lineage does not occur in EMR elevated areas (Fig. 2), occupying only adjacent lowland areas of the east and north side of the EMR. The poorly resolved relationships within the Northeast lineage subclades (Fig. S3, Supporting information) may be attributed to the reduced topographic

complexity of the Caatinga (Sampaio 1995) that potentially enhances opportunity for gene flow. In addition, this lineage coalesces recently for all genes, in agreement with recent population expansion and the lower nucleotide diversity (Table 1 and Fig. 3). A similar pattern was reported for geckos of the *Phyllopezus pollicaris* complex in which the Caatinga lineages showed lower genetic diversity and weaker structure than the Cerrado lineages (Werneck *et al.* 2012). Other widespread lineages from the Caatinga have also revealed weaker genetic structure, including plants (Caetano *et al.* 2008) and frogs (São Pedro unpublished data).

The mtDNA and nuDNA haplotype genealogies indicated clear genetic structure between Northeast and Southwest lineages, although there is some mixing of individuals in all genes (Fig. 3). Some haplotype sharing can potentially be explained by retention of ancestral polymorphism (Knowles & Carstens 2007) because very distant localities (São Gonçalo do Amarante no. 10, Nova Olinda no. 27, and Montezuma no.75; see Fig. 1) share the same mtDNA ancestral haplotype (H93; see Fig. 3 and Table S6, Supporting information). Signal of incomplete lineage sorting can also be found in all nuclear genes (e.g. RP40: H10; R35: H1; ATPSB: H35; and NKTR: H17). Conversely, significant migration detected by IMA2 can potentially explain the sharing of derived mtDNA haplotypes (e.g. H21) among close localities (Alagoado no. 43 and Casa Nova no. 44; see Fig. 1). Nuclear networks also show some evidence of migration (e.g. R35: H5 and H6; ATPSB: H26, H32 and H37; NKTR: H23 and H44).

Several other studies have reported cases of speciation with gene flow (e.g. Martin *et al.* 2013; Myers *et al.* 2013; Ruane *et al.* 2014). Although such cases may contradict common sense, it may be more common than previously thought (Nosil 2008) and the present study represents one more example. Our multilocus population assignment showed a clear and strong genetic break between Northeast and Southwest lineages. Further, the mtDNA genetic



distance between them (uncorrected p-distance of 3.6% and  $F_{ST}$  of 46%) is consistent with genetic distances among closely related yet distinct species of squamates (e.g. D'angiolella *et al.* 2011; Rodrigues *et al.* 2013; Teixeira *et al.* 2013). Therefore, our molecular results suggest that the two lineages represent two distinct species.

### *Taxonomic implications*

Among the currently recognized 14 species within the *C. ocellifer* group (see species list in Arias *et al.* 2014), six are partially or totally distributed in the Caatinga domain [i.e. *C. confusionibus* (Arias *et al.* 2011a), *C. cyanurus* (Arias *et al.* 2011b), *C. nigrigula* (Arias *et al.* 2011b), *C. ocellifer* (Spix 1825), *C. pyrrhogularis* (Silva & Ávila-Pires 2013), and *C. venetacaudus* (Arias *et al.* 2011a)]. Two of these species (*C. cyanurus* and *C. venetacaudus*) can be easily distinguished based on morphological characteristics and distinct color patterns (Arias *et al.* 2011a, b). *Cnemidophorus venetacaudus* (used as outgroup) was also genetically distinguishable from all our other samples. In contrast, some individuals included in our analyses (EE Raso da Catarina/BA: N299, N301, N309; Paulo Afonso/BA: N458; Canindé de São Francisco/SE: N459, N460, N463; Poço Redondo/SE: N455, N457; and Nossa Senhora da Glória/SE: N495, N497; see Table S6, Supporting information) present some morphological characteristics stated as diagnostic of *C. nigrigula* (see Garda *et al.* 2013). Likewise, we also sequenced specimens attributable to *C. confusionibus* (Rio Grande do Piauí/PI: N475; D. O. Mesquita, pers. com.) based on lepidosis (Arias *et al.* 2011a). Still, these samples were not genetically distinguishable from our Northeast species. Therefore, we recommend a more detailed investigation on the identity of *C. nigrigula* and *C. confusionibus* by incorporating genetic samples from their type-localities. Another newly described species from northern Piauí state (*C. pyrrhogularis* Silva & Ávila-Pires 2013) is not easily distinguishable from *C. ocellifer*. Our samples from the range of *C. pyrrhogularis* (localities

from Piauí state available at Tables S1 and S6) did not cluster in any exclusive lineage neither showed other signals of genetic particularities that justify its recognition as a separate species. In fact, we sequenced specimens with both morphological patterns attributed by Silva & Ávila-Pires (2013) to *C. pyrrhogularis* and *C. cf. ocellifer*, and they were genetically indistinguishable. Hence, our findings suggest that Northeast species and *C. pyrrhogularis* correspond to the same species. Although the type-locality of *C. ocellifer* is simply referred to as ‘Bahia’ in the species description (Spix 1825), Vanzolini (1981) indicated Salvador, the capital of Bahia state, as its type-locality after a detailed study on Spix and Martius’ expedition to Brazil. In fact, Salvador is frequently referred to as Bahia in the books reporting the Bahia expedition (Spix & Martius 1976) and subsequent studies on *Cnemidophorus* taxonomy have followed Vanzolini’s assumption (e.g. Rocha *et al.* 2000; Silva & Ávila-Pires 2013). Therefore, we assume that *C. ocellifer* corresponds to our Northeast species and *C. pyrrhogularis* is a junior synonym of this taxon. Finally, the holotype of *C. ocellifer* is considered lost (Hoogmoed & Gruber 1983; Franzen & Glaw 2007) and a neotype designation is warranted. Further work to designate a neotype is needed to stabilize the taxonomy of the group.

The Southwest species includes the most recently described species, *Cnemidophorus xacriaba* (Arias *et al.* 2014). Some specimens present in our analyses (São Desidério/BA: N753, N757; see Tables S1 and S6, Supporting information) were also analyzed in the *C. xacriaba* description paper. We also sequenced a sample from its type-locality (PARNA Cavernas do Peruaçu/MG: N774). However, our revealed distributional range of Southwest species suggests a wider occurrence area for *C. xacriaba*. Contrasting with the species description paper, *C. xacriaba* is not endemic to the Planalto dos Gerais, reaching further east through the right bank of the SFR up to higher elevations along the EMR. *Cnemidophorus xacriaba* also occurs further north to central-west Piauí state (e.g. Uruçuí-Una no. 38).

Therefore, *C. xacriaba* is not a Cerrado endemic species as previously assumed (Arias *et al.* 2014), but also occurs in several localities along the southwest Caatinga. It is likely that *C. xacriaba* is also more widespread in Cerrado biome and its distribution range should be investigated. Hence, other populations formerly designated as *C. ocellifer* from central Brazil (Arias *et al.* 2014) are most likely our Southwest species (i.e. *C. xacriaba*) or other still undescribed taxa.

Although our aim was not focused on morphological data, it is worthwhile to underscore that specimens used in our analyses and directly collected by us (~ 240 samples) showed a remarkable color variation that did not follow clear genetic differences. Because most descriptions of *Cnemidophorus* species are based solely on morphological data, we strongly recommend caution in the use of color patterns as diagnostic characteristics and an appropriate evaluation of geographic variation in comparisons. Instead of representing real species-specific patterns, color variation may reflect high phenotypic plasticity, which could be selected for in a highly unpredictable environment like the Caatinga. Neutral processes as range expansion may also help to generate color variation (see Gehara *et al.* 2013). High polymorphism in color and scale patterns was also detected in another lizard genus from Caatinga (*Vanzosaura*, Recoder *et al.* 2014). The possible relationship between Caatinga lineages polymorphism and environmental variation or range expansion needs further investigation. Therefore, we encourage the use of multilocus molecular data in species descriptions, since this provides unequivocal evidence for genetic isolation. Moreover, coalescent-based species delimitation is a nonsubjective method, can be replicated and allows the test of alternative hypotheses of species limits by collecting homologous genetic loci from additional individuals (Fujita *et al.* 2012).

### *Species synonymy and distribution*

*Teius ocellifer*, Spix 1825: 23

*Cnemidophorus hygomi*, Reinhardt & Lütken 1862: 231

*Cnemidophorus ocellifer*, Peters 1877

*Cnemidophorus ocellifer*, Peters et al. 1970: 95

*Cnemidophorus ocellifer*, Cei 1993

*Cnemidophorus ocellifer*, Dirksen & De La Riva 1999

*Ameivula ocellifera*, Harvey et al. 2012

*Cnemidophorus* cf. *ocellifer*, Silva & Ávila-Pires 2013

*Cnemidophorus pyrrhogularis*, Silva & Ávila-Pires 2013. **New synonymy.**

Distribution: *Cnemidophorus ocellifer* occurs from north to southeastern Caatinga, occupying a large part of this biome, as well as coastal areas of northeastern Brazil under the Atlantic Forest domain (Fig. 2). Apparently, *C. ocellifer* does not reach the Cerrado, but small portions of the Amazonia biome (e.g. Alcântara no. 1; Figs 1 and 2) may be present in its northwestern-most distribution.

### **Conclusion**

We conducted a detailed phylogeographic assessment of the *Cnemidophorus ocellifer* species complex from the Caatinga and adjacent areas through the coupling of multilocus data, coalescent methods, historical demographic reconstructions, and model testing. This integrative approach is particularly relevant for poorly studied regions, such as the Caatinga xeric biome. We found that *C. ocellifer* species complex from the Caatinga is composed of two distinct species associated with different geographic regions. Our data support a speciation with gene flow and highlight the role of the environmental gradients in the

diversification process. More precisely, the central-northern Caatinga region served as important center of origin, harboring the more ancient lineages. Our findings also indicate that researchers should exercise caution when using only morphological data for species diagnoses, especially when the precise ranges of species being compared are not known. The biodiversity assessment that results from this study provides essential information by identifying and delimiting areas with singular evolutionary histories and proposing a mechanism to generate early Caatinga biota.

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### Author contributions

E.F.O. and G.C.C. conceived the initial idea of the study. E.F.O., V.A.S.P., D.O.M., A.A.G., G.R.C., M.T.R., F.J.A., H.Z., and R.M.L.S. collected the samples. E.F.O., V.A.S.P., X.C. and E.A.M. generated the sequence data. E.F.O., M.G., V.A.S.P., X.C., and E.A.M. performed the analyses. E.F.O., M.G., V.A.S.P., F.T.B., D.O.M., A.A.G., G.R.C., and G.C.C. contributed to writing paper. All authors commented and improved the final version of the manuscript.

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## Tables and Figures

Table 1. Genetic statistics for each locus for Northeast and Southwest lineages of *Cnemidophorus ocellifer*.

Locus	Population	L (bp)	N	S	H	Hd	$\pi$	Tajima's D	P value
12S	Northeast	370	330	66	103 (102)	0.947	0.01732	-1.29179	P > 0.10
	Southwest	370	68	47	34 (33)	0.967	0.02133	-1.6959	P > 0.10
ATPSB	Northeast	623	206*	32	35 (33)	0.830	0.00411	-1.49981	P > 0.10
	Southwest	623	46*	32	27 (25)	0.954	0.00984	-0.53478	P > 0.10
NKTR	Northeast	354	190*	24	41 (40)	0.647	0.00408	-1.79457	P < 0.05**
	Southwest	354	40*	17	22 (21)	0.937	0.01039	-0.42723	P > 0.10
R35	Northeast	396	220*	12	13 (11)	0.592	0.00178	-1.56108	0.10 > P > 0.05
	Southwest	396	48*	9	11 (9)	0.809	0.00421	-0.50002	P > 0.10
RP40	Northeast	354	216*	5	6 (4)	0.547	0.00185	-0.41487	P > 0.10
	Southwest	354	48*	11	11 (9)	0.793	0.00634	-0.27788	P > 0.10

L: length in base pairs; N: sample size; S: number of polymorphic sites; H: number of haplotypes (number of exclusive haplotypes in this lineage); Hd: haplotype diversity;  $\pi$ : nucleotide diversity; Tajima's D tests and P values; \*phased sequences; \*\*significant.

Table 2. Variance percentages for components of analyses of molecular variance (AMOVA) performed with different genes in Northeast and Southwest lineages of *Cnemidophorus ocellifer*.

<b>Locus</b>	<b>Source of variation</b>		<b>F<sub>ST</sub></b>
	<b>Between lineages</b>	<b>Within lineages</b>	
12S	46.16	53.84	0.46158
ATPSB	58.89	41.11	0.58893
NKTR	55.47	44.53	0.55466
RP40	66.18	33.82	0.66179
R35	28.36	71.64	0.28359

all *P* values < 0.0001.

Table 3. Genetic distance (uncorrected p-distance) between and within Northeast and Southwest lineages of *Cnemidophorus ocellifer* performed with different genes.

Locus	Between	Within	
		Northeast	Southwest
12S	0.036	0.018	0.022
ATPSB	0.015	0.004	0.010
NKTR	0.014	0.004	0.011
R35	0.004	0.002	0.004
RP40	0.009	0.002	0.006

Table 4. Results from ABC analyses assuming four scenarios of diversification (A, B, C, or D; see Fig. 6) between Northeast and Southwest lineages of *Cnemidophorus ocellifer*. Values represent posterior probabilities of comparisons within each scenario (tolerance of 0.0001) and among the best models selected for each scenario (tolerance of 0.001). Preferred model at each comparison is highlighted in bold.

Scenario	Model	Regression method	
		mnlogistic	neuralnet
A	BeastCM	0	0
	BeastSC	0	0
	IMaCM	0.0002	0.0027
	IMaSC	<b>0.9998</b>	<b>0.9973</b>
B	BeastCM	0.1481	<b>0.4150</b>
	BeastSC	0.1166	0.3841
	IMaCM	<b>0.6912</b>	0.1566
	IMaSC	0.0441	0.0443
C	BeastCM	0.1709	0.0583
	BeastSC	0.2375	0.1923
	IMaCM	<b>0.3884</b>	<b>0.5969</b>
	IMaSC	0.2031	0.1525
D	BeastCM	0	0.0012
	BeastSC	0	0
	IMaCM	<b>0.9892</b>	<b>0.9006</b>
	IMaSC	0.0108	0.0982
A	IMaSC	**	0
B	BeastCM	0	0
B	IMaCM	0	0
C	IMaCM	0.0001	0
D	IMaCM	<b>0.9999</b>	<b>1</b>

Model: IMa2 divergence time (IMa), \*BEAST divergence time (Beast), recent migration (secondary contact, SC), and migration throughout the population history (constant migration, CM); \*\*zero simulations accepted in the rejection step, and therefore, the model was not included in the regression step.

Fig. 1. Distribution of sampled localities for *Cnemidophorus ocellifer* species complex. Numbers correspond to 78 localities names in Tables S1 and S6, Supporting information. Gray shades represent biomes limits: Caatinga (Ca) in dark gray and Cerrado (Ce) in light gray.

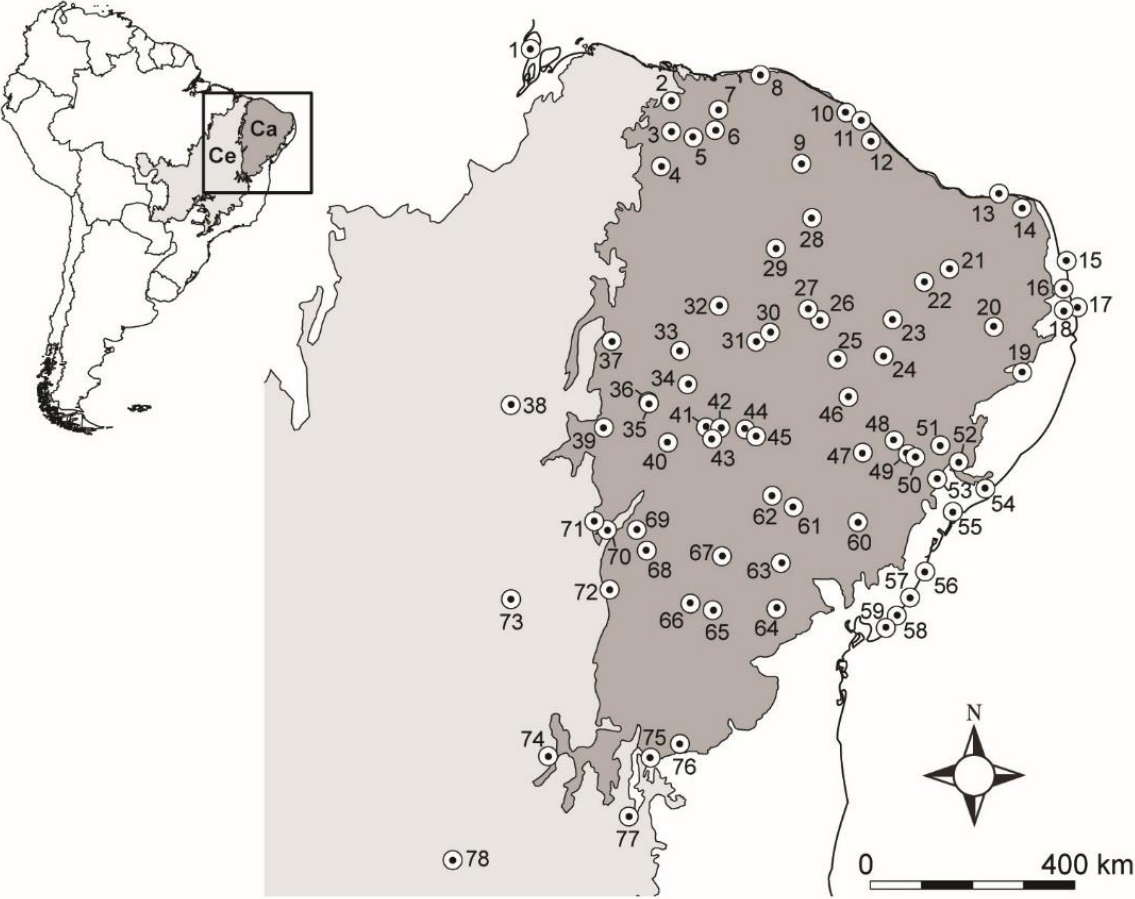




Fig. 2. GENELAND analysis (A and B) with posterior probability isoclines, which indicate extensions of the genetic populations found (black lines with inclusion probabilities). Light color zones in each map indicate the groups of localities with greater probabilities of belonging to the same genetic unit. Black dots indicate locations of the 78 analyzed localities. Map on the right (C) shows the distribution of Northeast (white circles) and Southwest (gray circles) lineages along Caatinga (Ca) and Cerrado (Ce) biomes, depicting São Francisco River (a), its hypothetical paleo-course (b), and Espinhaço Mountain Range (c). Red dotted circle represents the probable geographic origin of Northeast lineage (see also Fig. 5). Green color represents higher altitudes and white represents lower altitudes.

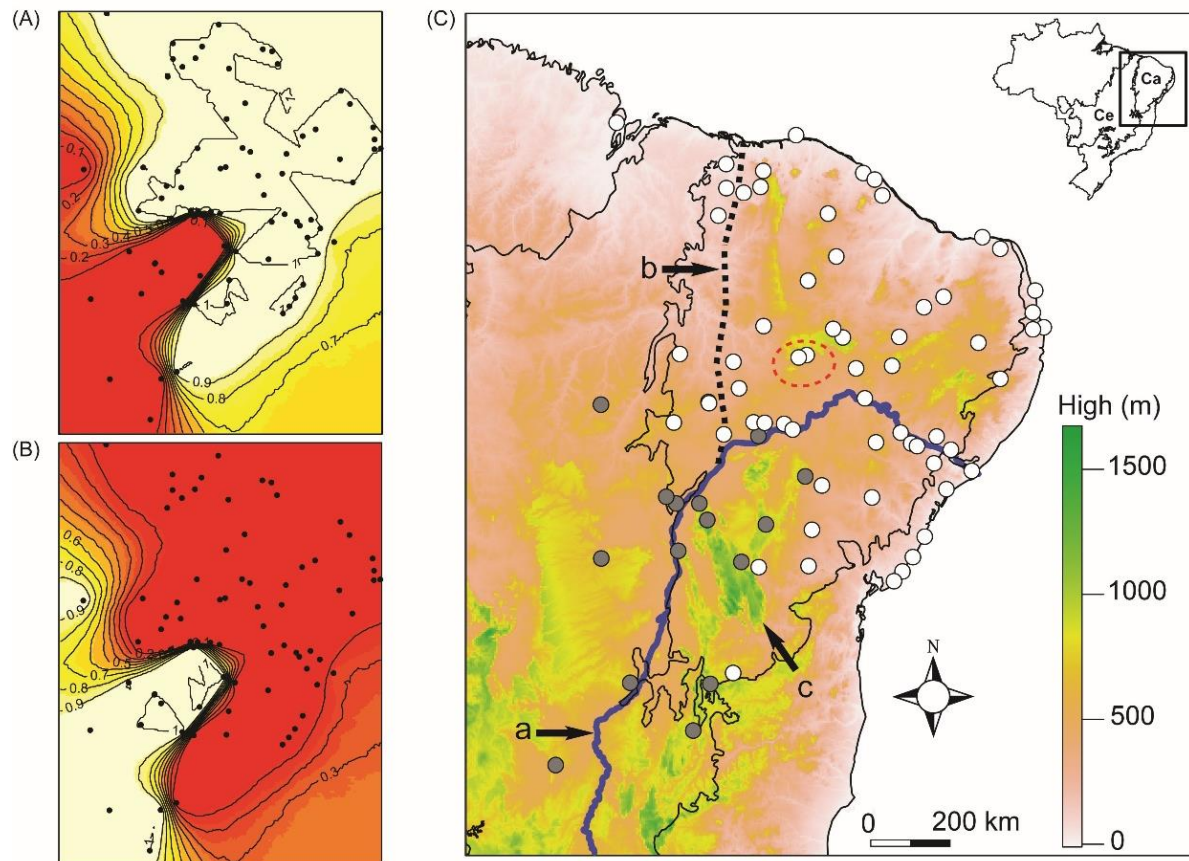


Fig. 3. Haplotype genealogies from maximum likelihood analysis of 12S (A), RP40 (B), R35 (C), ATPSB (D), and NKTR (E) gene trees performed in the software Haploviewer. Each haplotype is represented by a circle whose area is proportional to its frequency (indicated in legend). White and gray circles represent Northeast and Southwest lineages, respectively. Black dots represent inferred unsampled or extinct haplotypes. The localities where each haplotypes (coded as a number) occurs are available in Table S6, Supporting information.

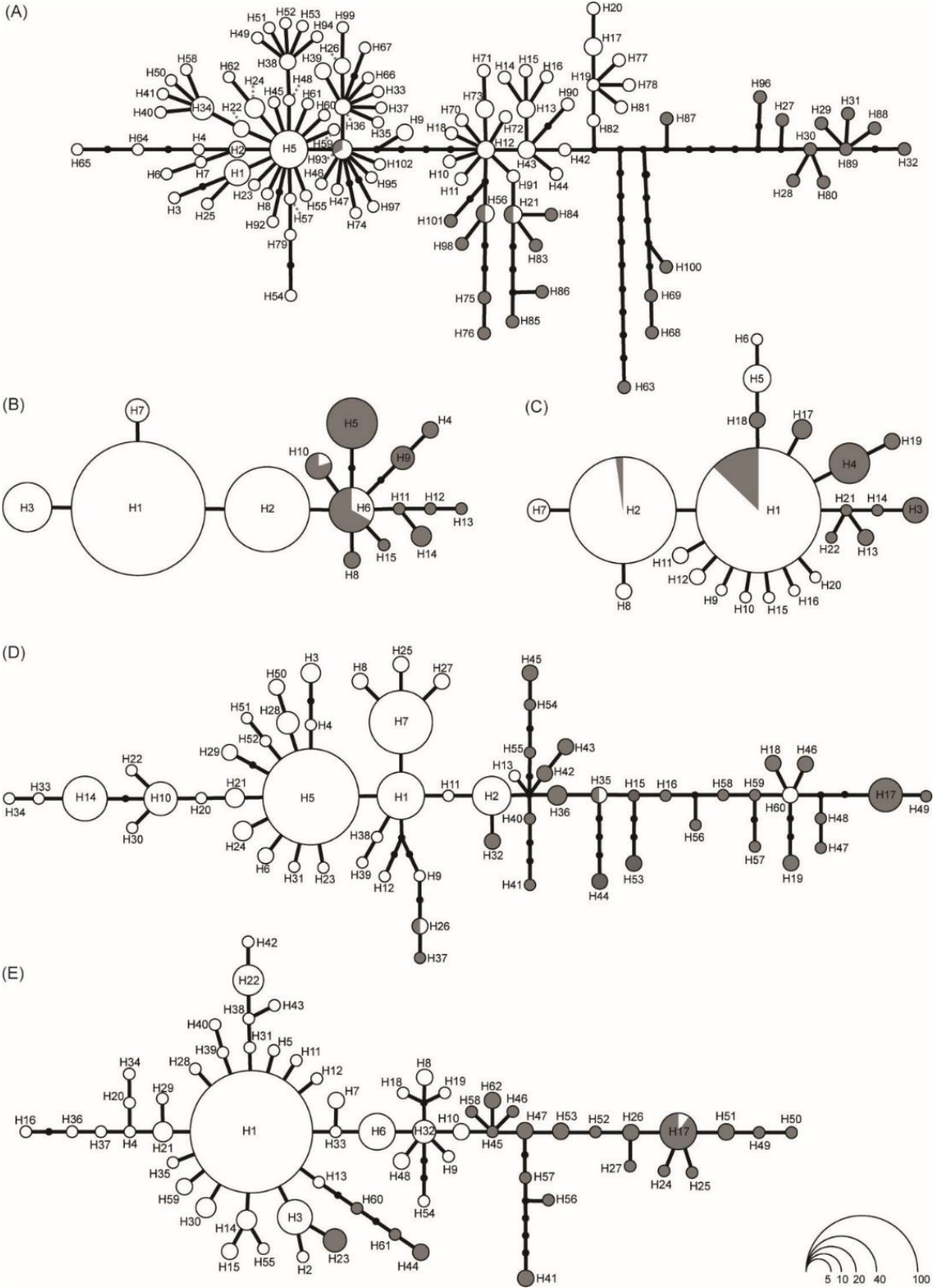


Fig. 4. Bayesian Skyline plots illustrating effective population sizes ( $N_e$ ) through time (in years) of Southwest (A) and Northeast (B) lineages. The back line represents the median population size, and the gray lines represent 95% higher posterior probability.

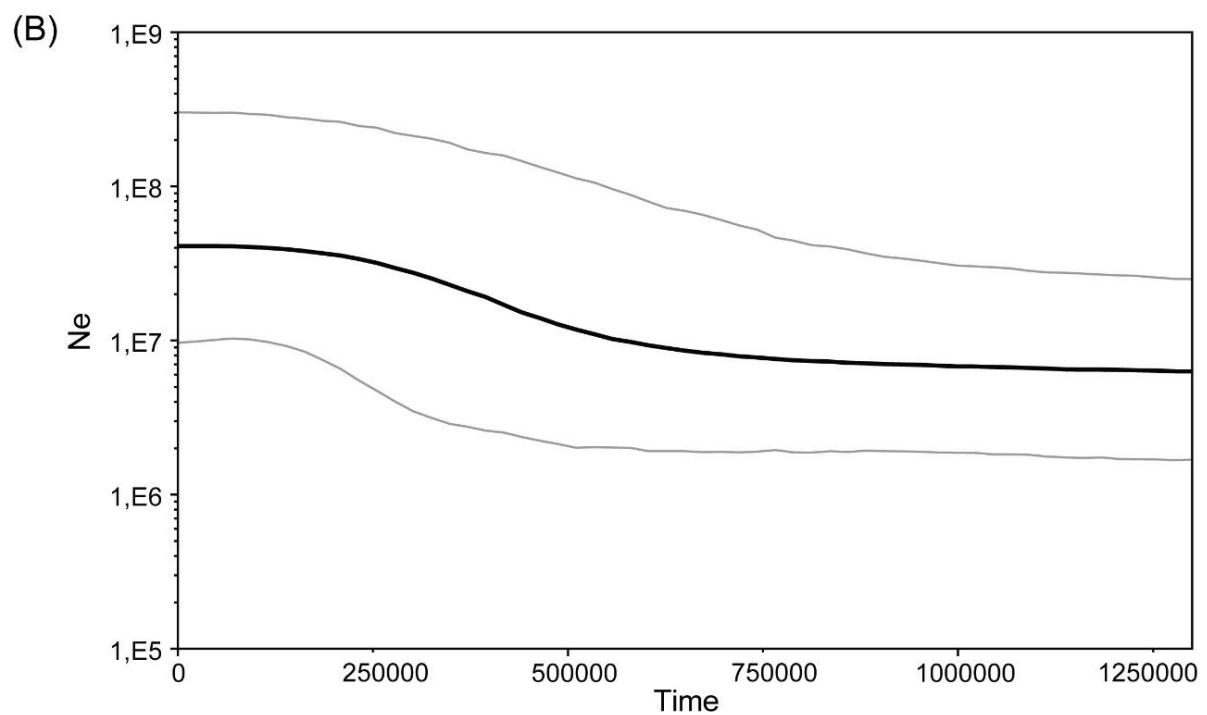
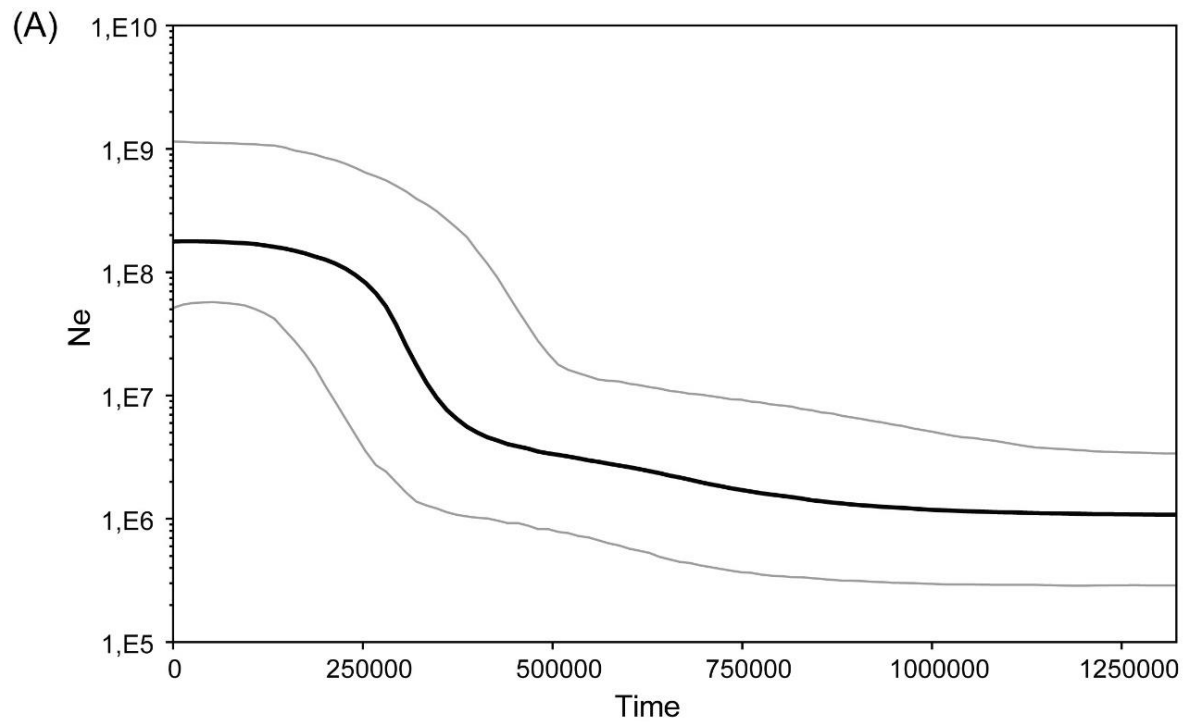


Fig. 5. Phylogeographic reconstructions of Northeast lineage. The spatiotemporal dynamics for the genes 12S (A), ATPSB (B), NKTR (C), R35 (D), and RP40 (E) are shown in four different time frames since their origin to present. Light polygons represent basal clades and darker ones represent recent clades. Lines represent the maximum clade credibility tree branches projected on the surface. Maps are based on satellite pictures visualized with Google Earth.

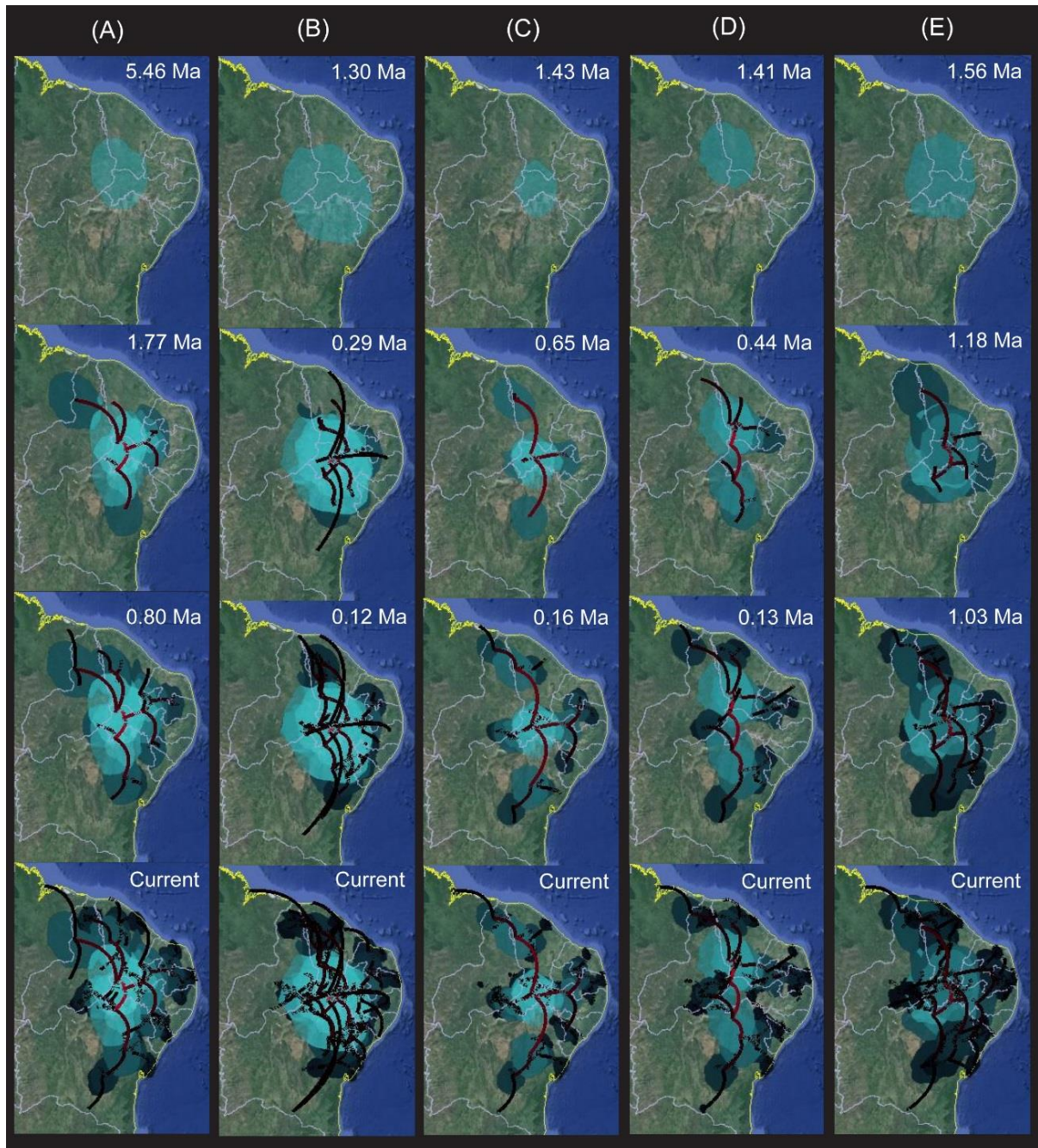
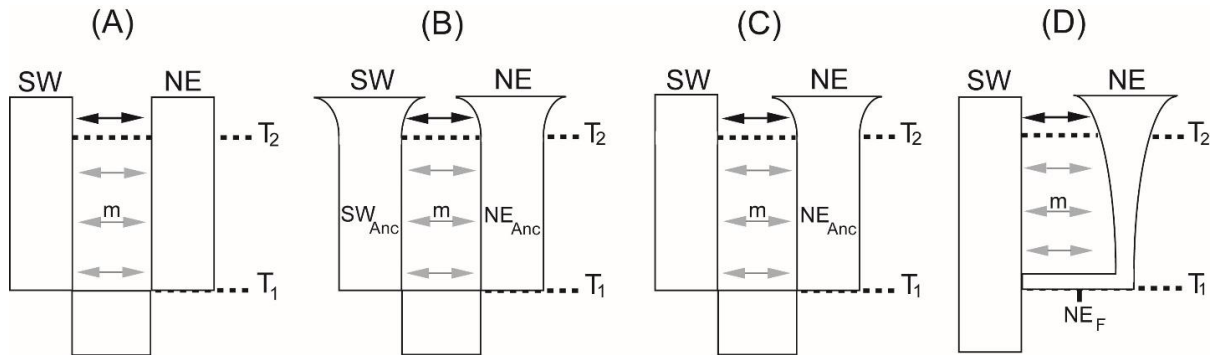


Fig. 6. Alternative scenarios for diversification of the Northeast (NE) and Southwest (SW) lineages tested with multilocus ABC. Divergence time is referred to as  $T_1$ , and  $SW_{ANC}$  and  $NE_{ANC}$  represent Southwest and Northeast ancestral populations, respectively. Northeast founder population is referred to as  $NE_F$ . Models include two migration rates ( $m$ ) possibilities: migration throughout the population history (gray and black arrows, and migration starts in  $T_1$ ) and recent migration (black arrows, and migration starts in  $T_2$ ).  $T_2$  also represents the beginning of the population expansion (scenarios B and C). Prior distributions for each parameter are available at Table S5, Supporting information. See Materials and Methods for more details.



## Supplementary Material

### Taxonomic Background

*Cnemidophorus* genus encompass four species groups: the *C. lemniscatus* group, *C. lacertoides* group, *C. longicauda* group, and *C. ocellifer* group (Arias *et al.* 2011a). These lizards are distributed in South America from Lesser Antilles (near Venezuela) to southern Argentina (Arias *et al.* 2011a; Arias *et al.* 2014a). A recent taxonomic review of Teiidae based on morphological data (Harvey *et al.* 2012) corroborated previous molecular studies (Giugliano *et al.* 2006; Reeder *et al.* 2002) in recognizing *Cnemidophorus* as non-monophyletic. To resolve the polyphyly, Harvey *et al.* (2012) proposed new genera to three of the four groups.

*Ameivula* was created to encompass all species included in the *C. ocellifer* group (Harvey *et al.* 2012). However, the diagnosis proposed for *Ameivula* is problematic because the characters used are variable within the genus (see Arias *et al.* 2014b). Additionally, some of the new taxonomic rearrangements proposed by Harvey *et al.* (2012) have been considered premature (Giugliano *et al.* 2013). To favor taxonomic stability, we reject the propositions made by Harvey *et al.* (2012) and consider the species included in the *C. ocellifer* group as still belonging to the genus *Cnemidophorus*.

*Cnemidophorus ocellifer* group encompass currently 14 species (see species list in Arias *et al.* 2014b). Most of these species can be clustered in two subgroups (i.e. *C. littoralis* and *C. ocellifer* subgroups) based on morphological characteristics (Arias *et al.* 2011a, b; Arias *et al.* 2014a; Arias *et al.* 2014b; Silva & Ávila-Pires 2013). *Cnemidophorus ocellifer* is the most widespread species of *C. ocellifer* subgroup and its presumed occurrence is from northeastern Brazil to Mato Grosso do Sul state (Arias *et al.* 2014b). Because of its remarkable color and lepidosis variation, *C. ocellifer* is considered a species complex (e.g. Arias *et al.* 2014b; Harvey *et al.* 2012; Rocha *et al.* 1997; Rodrigues 2003).

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## Fossil Record

We conducted a review of Teiidae fossils to justify our fossil calibration. The earliest record of Teiidae dates from the early Eocene Itaboraian stratigraphic levels (56–53 Ma) from Rio de Janeiro, Brazil (more details in Albino & Brizuela 2014). Other important record is an extinct tupinambine from Lumbreira Formation in northwestern Argentina (Casamayoran ages; 45.5–38 Ma). The presence of a tupinambine from the early Eocene indicates that the divergence of the two subfamilies (Teiinae and Tupinambinae) had already occurred at that time (Albino & Brizuela 2014). *Paradracaena* is another extinct tupinambine from the mid Miocene Laventan fauna (13.8–11.8 Ma) of Colombia and is considered the sister taxon of extant *Dracaena* (Albino & Brizuela 2014). *Tupinambis* fossils are the earliest representative of extant Teiidae and come from the fossil-bearing beds of the Colhuehuapian (21–19.5 Ma) from the early Miocene in Patagonia (Brizuela & Albino 2004). Records of *Tupinambis* are common and well represented in different deposits of South America in all subsequent epochs of Miocene (see examples in Brizuela & Albino 2004). The first record of Teiinae belongs to “cnemidophorines”, an informal group formed by genera *Ameiva*, *Aspidoscelis*, *Cnemidophorus*, and *Kentropyx* (i.e. non-*Teius* and *Dicrodon*) and considered monophyletic in some molecular studies (e.g. Giugliano *et al.* 2007; Reeder *et al.* 2002) but not in others (e.g. Pyron *et al.* 2013). Paleontological and morphological studies recognize some differences between this informal group and the two other genera of this subfamily (Albino *et al.* 2013; Brizuela & Albino 2010). On the other hand, it is not possible to assign the fossil to any cnemidophorine genus (Albino *et al.* 2013). Cnemidophorines first appeared in North America (Florida) in the early Hemingfordian (20.4–15.9 Ma) from the early Miocene (Chovanec 2014; Estes & Báez 1985; Vanzolini & Heyer 1985). Finally, the oldest South American cnemidophorine fossil is dated at Chasicuan mammalian fauna (10–9 Ma) from the late Miocene in Argentina (Albino *et al.* 2013).

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## Tables and Figures

Table S1. Samples of *Cnemidophorus* used in present study (398 samples + 1 outgroup). For each sample is presented map code number (see Fig. 1), collection locality, state, institution of origin, voucher number, laboratory code number, and geographic coordinates (longitude and latitude in decimal degrees).

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
1	<i>Cnemidophorus ocellifer</i>	Alcântara	MA	USP	MRT9955	N658	-44.6151	-2.5213
2	<i>Cnemidophorus ocellifer</i>	Joaquim Pires	PI	UFRN	EFO70	N100	-42.1087	-3.4538
3	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO73	N103	-42.104	-3.9974
3	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO74	N104	-42.104	-3.9974
3	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO75	N105	-42.104	-3.9974
3	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO76	N106	-42.104	-3.9974
3	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO78	N108	-42.104	-3.9974
3	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO79	N109	-42.104	-3.9974
4	<i>Cnemidophorus ocellifer</i>	Nossa Senhora de Nazaré	PI	UFRN	EFO80	N110	-42.2878	-4.6175
4	<i>Cnemidophorus ocellifer</i>	Nossa Senhora de Nazaré	PI	UFRN	EFO81	N111	-42.2878	-4.6175
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60733	N7	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60734	N8	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60735	N9	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60736	N10	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60737	N11	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60738	N12	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60739	N13	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60740	N14	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60742	N16	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60743	N17	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60747	N18	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60748	N19	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60749	N20	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60750	N21	-41.708	-4.1014
5	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60751	N22	-41.708	-4.1014
6	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO82	N112	-41.323	-3.9692
6	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO83	N113	-41.323	-3.9692

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
6	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO84	N114	-41.323	-3.9692
6	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO86	N116	-41.323	-3.9692
6	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO87	N117	-41.323	-3.9692
6	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO88	N118	-41.323	-3.9692
7	<i>Cnemidophorus ocellifer</i>	Viçosa do Ceará	CE	UFC	Tec1909	N526	-41.2605	-3.6083
8	<i>Cnemidophorus ocellifer</i>	Jericoacoara	CE	USP	PN57	N776	-40.5103	-2.8017
8	<i>Cnemidophorus ocellifer</i>	Jericoacoara	CE	USP	PN58	N777	-40.5103	-2.8017
8	<i>Cnemidophorus ocellifer</i>	Jericoacoara	CE	USP	PN59	N778	-40.5103	-2.8017
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB382	N393	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB406	N394	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB439	N395	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB540	N397	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB550	N398	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB832	N399	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB833	N400	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB965	N402	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB980	N403	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB990	N405	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB993	N406	-39.779	-4.5715
9	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB994	N407	-39.779	-4.5715
10	<i>Cnemidophorus ocellifer</i>	São Gonçalo do Amarante	CE	UFRN	EFO50	N81	-38.974	-3.6568
10	<i>Cnemidophorus ocellifer</i>	São Gonçalo do Amarante	CE	UFRN	EFO53	N84	-38.974	-3.6568
10	<i>Cnemidophorus ocellifer</i>	São Gonçalo do Amarante	CE	UFRN	EFO54	N85	-38.974	-3.6568
10	<i>Cnemidophorus ocellifer</i>	São Gonçalo do Amarante	CE	UFRN	EFO55	N86	-38.974	-3.6568
11	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec3159	N528	-38.711	-3.8041
11	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec3175	N529	-38.711	-3.8041
11	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec3210	N530	-38.711	-3.8041
11	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec941	N522	-38.711	-3.8041
11	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec942	N523	-38.711	-3.8041
12	<i>Cnemidophorus ocellifer</i>	Pacajus	CE	UFC	Tec934	N521	-38.5371	-4.1638
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC10	N509	-36.249	-5.1042
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC11	N510	-36.249	-5.1042
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC16	N511	-36.249	-5.1042
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC2	N502	-36.249	-5.1042

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC3	N503	-36.249	-5.1042
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC4	N504	-36.249	-5.1042
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC6	N505	-36.249	-5.1042
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC7	N506	-36.249	-5.1042
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC8	N507	-36.249	-5.1042
13	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC9	N508	-36.249	-5.1042
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	AAGARDA5601	N331	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	AAGARDA5605	N332	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	AAGARDA5606	N333	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	AAGARDA5607	N334	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	AAGARDA5611	N336	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	AAGARDA5613	N337	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	AAGARDA5621	N339	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	AAGARDA5622	N340	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	AAGARDA5775	N346	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFPB	FSCHUFPB2510	N445	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFPB	FSCHUFPB2541	N448	-35.839	-5.3651
14	<i>Cnemidophorus ocellifer</i>	João Camara	RN	UFRN	MV15	N377	-35.839	-5.3651
15	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2052	N421	-35.04	-6.3072
15	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2053	N422	-35.04	-6.3072
15	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2055	N424	-35.04	-6.3072
15	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2064	N429	-35.04	-6.3072
15	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2065	N430	-35.04	-6.3072
15	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2319	N434	-35.04	-6.3072
15	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2320	N435	-35.04	-6.3072
15	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2323	N438	-35.04	-6.3072
15	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2326	N440	-35.04	-6.3072
16	<i>Cnemidophorus ocellifer</i>	Rio Tinto	PB	UFPB	FSCHUFPB199	N389	-35.0950	-6.8022
16	<i>Cnemidophorus ocellifer</i>	Rio Tinto	PB	UFPB	FSCHUFPB200	N390	-35.0950	-6.8022
16	<i>Cnemidophorus ocellifer</i>	Rio Tinto	PB	UFPB	FSCHUFPB201	N391	-35.0950	-6.8022
17	<i>Cnemidophorus ocellifer</i>	João Pessoa	PB	UFPB	FSCHUFPB1121	N408	-34.8428	-7.1366
18	<i>Cnemidophorus ocellifer</i>	Cruz do Espírito Santo	PB	UFPB	L406	N501	-35.0925	-7.1826
19	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO190	N204	-35.836	-8.2986
19	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO191	N205	-35.836	-8.2986

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
19	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO192	N206	-35.836	-8.2986
19	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO194	N208	-35.836	-8.2986
19	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO195	N209	-35.836	-8.2986
19	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO197	N211	-35.836	-8.2986
20	<i>Cnemidophorus ocellifer</i>	Cabaceiras	PB	UFPB	FSCHUFPB2042	N415	-36.3399	-7.4853
20	<i>Cnemidophorus ocellifer</i>	Cabaceiras	PB	UFPB	FSCHUFPB2043	N416	-36.3399	-7.4853
20	<i>Cnemidophorus ocellifer</i>	Cabaceiras	PB	UFPB	FSCHUFPB2049	N420	-36.3399	-7.4853
21	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO11	N51	-37.135	-6.4482
21	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO13	N53	-37.135	-6.4482
21	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO14	N54	-37.135	-6.4482
21	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO6	N47	-37.135	-6.4482
21	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO7	N48	-37.135	-6.4482
21	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO8	N49	-37.135	-6.4482
22	<i>Cnemidophorus ocellifer</i>	Vista Serrana	PB	UFRN	EFO15	N55	-37.5863	-6.6830
22	<i>Cnemidophorus ocellifer</i>	Vista Serrana	PB	UFRN	EFO9	N50	-37.5863	-6.6830
23	<i>Cnemidophorus gr. ocellifer</i>	Itaporanga	PB	UnB	CHUNB61927	N23	-38.1494	-7.3534
24	<i>Cnemidophorus gr. ocellifer</i>	Serra Talhada	PE	UFPB	FRD1067	N490	-38.313	-8.0039
24	<i>Cnemidophorus gr. ocellifer</i>	Serra Talhada	PE	UFPB	FRD1068	N491	-38.313	-8.0039
24	<i>Cnemidophorus gr. ocellifer</i>	Serra Talhada	PE	UFPB	FRD1069	N492	-38.313	-8.0039
24	<i>Cnemidophorus gr. ocellifer</i>	Serra Talhada	PE	UFPB	FRD1074	N493	-38.313	-8.0039
24	<i>Cnemidophorus gr. ocellifer</i>	Serra Talhada	PE	UFPB	FRD1098	N494	-38.313	-8.0039
25	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO100	N128	-39.137	-8.0628
25	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO102	N130	-39.137	-8.0628
25	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO103	N131	-39.137	-8.0628
25	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO104	N132	-39.137	-8.0628
25	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO108	N136	-39.137	-8.0628
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64550	N28	-39.441	-7.3658
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64554	N31	-39.441	-7.3658
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64555	N32	-39.441	-7.3658
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64557	N34	-39.441	-7.3658
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64558	N35	-39.441	-7.3658
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64560	N37	-39.441	-7.3658
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64561	N38	-39.441	-7.3658
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64562	N39	-39.441	-7.3658

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64564	N41	-39.441	-7.3658
26	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64565	N42	-39.441	-7.3658
27	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11903	N708	-39.66	-7.1716
27	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11905	N709	-39.66	-7.1716
27	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11906	N710	-39.66	-7.1716
27	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11907	N711	-39.66	-7.1716
27	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11908	N712	-39.66	-7.1716
27	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11909	N713	-39.66	-7.1716
28	<i>Cnemidophorus ocellifer</i>	Mineirópolis	CE	UFRN	EFO23	N61	-39.5890	-5.5392
28	<i>Cnemidophorus ocellifer</i>	Mineirópolis	CE	UFRN	EFO24	N62	-39.5890	-5.5392
28	<i>Cnemidophorus ocellifer</i>	Mineirópolis	CE	UFRN	EFO28	N66	-39.5890	-5.5392
29	<i>Cnemidophorus ocellifer</i>	Tauá	CE	UFRN	EFO34	N72	-40.237	-6.0853
29	<i>Cnemidophorus ocellifer</i>	Tauá	CE	UFRN	EFO35	N73	-40.237	-6.0853
29	<i>Cnemidophorus ocellifer</i>	Tauá	CE	UFRN	EFO36	N74	-40.237	-6.0853
29	<i>Cnemidophorus ocellifer</i>	Tauá	CE	UFRN	EFO37	N75	-40.237	-6.0853
30	<i>Cnemidophorus gr. ocellifer</i>	Trindade	PE	UFPB	FRD927	N477	-40.277	-7.7452
30	<i>Cnemidophorus gr. ocellifer</i>	Trindade	PE	UFPB	FRD928	N478	-40.277	-7.7452
30	<i>Cnemidophorus gr. ocellifer</i>	Trindade	PE	UFPB	FRD929	N479	-40.277	-7.7452
30	<i>Cnemidophorus gr. ocellifer</i>	Trindade	PE	UFPB	FRD967	N485	-40.277	-7.7452
31	<i>Cnemidophorus ocellifer</i>	Nascente	PE	UFPB	FRD941	N480	-40.481	-7.8831
31	<i>Cnemidophorus ocellifer</i>	Nascente	PE	UFPB	FRD942	N481	-40.481	-7.8831
31	<i>Cnemidophorus ocellifer</i>	Nascente	PE	UFPB	FRD943	N482	-40.481	-7.8831
31	<i>Cnemidophorus ocellifer</i>	Nascente	PE	UFPB	FRD944	N483	-40.481	-7.8831
32	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO110	N137	-41.254	-7.1085
32	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO111	N138	-41.254	-7.1085
32	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO113	N140	-41.254	-7.1085
32	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO114	N141	-41.254	-7.1085
32	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO115	N142	-41.254	-7.1085
33	<i>Cnemidophorus ocellifer</i>	Simplício Mendes	PI	UFRN	EFO119	N145	-41.944	-7.9137
33	<i>Cnemidophorus ocellifer</i>	Simplício Mendes	PI	UFRN	EFO120	N146	-41.944	-7.9137
33	<i>Cnemidophorus ocellifer</i>	Simplício Mendes	PI	UFRN	EFO122	N148	-41.944	-7.9137
33	<i>Cnemidophorus ocellifer</i>	Simplício Mendes	PI	UFRN	EFO123	N149	-41.944	-7.9137
33	<i>Cnemidophorus ocellifer</i>	Simplício Mendes	PI	UFRN	EFO124	N150	-41.944	-7.9137
33	<i>Cnemidophorus ocellifer</i>	Simplício Mendes	PI	UFRN	EFO127	N153	-41.944	-7.9137

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
33	<i>Cnemidophorus ocellifer</i>	Simplício Mendes	PI	UFRN	EFO128	N154	-41.944	-7.9137
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV11	N583	-41.999	-8.6079
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV12	N584	-41.999	-8.6079
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV14	N585	-41.999	-8.6079
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV59	N596	-41.999	-8.6079
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV6	N582	-41.999	-8.6079
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV62	N597	-41.999	-8.6079
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV63	N598	-41.999	-8.6079
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV64	N599	-41.999	-8.6079
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV65	N600	-41.999	-8.6079
34	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV66	N601	-41.999	-8.6079
35	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO130	N155	-42.503	-8.8478
35	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO131	N156	-42.503	-8.8478
35	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO133	N158	-42.503	-8.8478
35	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO135	N160	-42.503	-8.8478
35	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO136	N161	-42.503	-8.8478
35	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO137	N162	-42.503	-8.8478
35	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO138	N163	-42.503	-8.8478
36	<i>Cnemidophorus</i> cf. <i>ocellifer</i>	PARNA Serra da Capivara	PI	UFRN	AAGARDA4702	N313	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5405	N314	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5419	N315	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5433	N316	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5439	N317	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5448	N320	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5449	N321	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5450	N322	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5466	N323	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5469	N324	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5470	N325	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5471	N326	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5473	N328	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5478	N329	-42.515	-8.8186
36	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5479	N330	-42.515	-8.8186
36	<i>Cnemidophorus venetacaudus</i> *	PARNA Serra da Capivara	PI	UFRN	AAGARDA5407	N779	-42.5150	-8.8186

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37	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Rio Grande do Piaui	PI	UFPB	FRD908	N475	-43.1701	-7.7385
38	<i>Cnemidophorus ocellifer</i>	Uruçuí-Una	PI	USP	MRT1614	N621	-44.9736	-8.8806
38	<i>Cnemidophorus ocellifer</i>	Uruçuí-Una	PI	USP	MRT1618	N622	-44.9736	-8.8806
38	<i>Cnemidophorus ocellifer</i>	Uruçuí-Una	PI	USP	MRT1666	N623	-44.9736	-8.8806
38	<i>Cnemidophorus ocellifer</i>	Uruçuí-Una	PI	USP	MRT1667	N624	-44.9736	-8.8806
38	<i>Cnemidophorus ocellifer</i>	Uruçuí-Una	PI	USP	MRT2106	N625	-44.9736	-8.8806
38	<i>Cnemidophorus ocellifer</i>	Uruçuí-Una	PI	USP	MRT2915	N626	-44.9736	-8.8806
38	<i>Cnemidophorus ocellifer</i>	Uruçuí-Una	PI	USP	MRT2961	N627	-44.9736	-8.8806
39	<i>Cnemidophorus ocellifer</i>	Caracol	PI	UFRN	EFO141	N166	-43.3068	-9.2842
39	<i>Cnemidophorus ocellifer</i>	Caracol	PI	UFRN	EFO145	N170	-43.3068	-9.2842
39	<i>Cnemidophorus ocellifer</i>	Caracol	PI	UFRN	EFO146	N171	-43.3068	-9.2842
40	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO148	N172	-42.163	-9.5503
40	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO149	N173	-42.163	-9.5503
40	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO150	N174	-42.163	-9.5503
40	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO152	N176	-42.163	-9.5503
40	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO153	N177	-42.163	-9.5503
40	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO154	N178	-42.163	-9.5503
41	<i>Cnemidophorus</i> sp.	Serra do Lajedo	BA	USP	MRT11761	N707	-41.4831	-9.2803
42	<i>Cnemidophorus</i> sp.	Atoleiro	BA	USP	MRT11750	N705	-41.2283	-9.2911
42	<i>Cnemidophorus</i> sp.	Atoleiro	BA	USP	MRT11751	N706	-41.2283	-9.2911
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11236	N672	-41.3722	-9.4861
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11237	N673	-41.3722	-9.4861
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11247	N674	-41.3722	-9.4861
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11248	N675	-41.3722	-9.4861
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11249	N676	-41.3722	-9.4861
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11250	N677	-41.3722	-9.4861
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11251	N678	-41.3722	-9.4861
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11232	N669	-41.3722	-9.4861
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11233	N670	-41.3722	-9.4861
43	<i>Cnemidophorus ocellifer</i>	Alagoado	BA	USP	MRT11235	N671	-41.3722	-9.4861
44	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO165	N179	-40.784	-9.3139
44	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO166	N180	-40.784	-9.3139
44	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO167	N181	-40.784	-9.3139
44	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO168	N182	-40.784	-9.3139



Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
44	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO171	N185	-40.784	-9.3139
44	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO172	N186	-40.784	-9.3139
44	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO174	N188	-40.784	-9.3139
44	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO176	N190	-40.784	-9.3139
44	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO177	N191	-40.784	-9.3139
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11225	N662	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11226	N663	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11227	N664	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11228	N665	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11229	N666	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11230	N667	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11231	N668	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3763	N651	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3764	N652	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3765	N653	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3766	N654	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3768	N655	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3769	N656	-40.588	-9.4428
45	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3770	N657	-40.588	-9.4428
46	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO178	N192	-38.937	-8.7384
46	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO180	N194	-38.937	-8.7384
46	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO182	N196	-38.937	-8.7384
46	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO183	N197	-38.937	-8.7384
46	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO186	N200	-38.937	-8.7384
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4105	N294	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4247	N296	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4296	N297	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4297	N298	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4302	N299	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4303	N300	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4304	N301	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4307	N304	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4318	N305	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4319	N306	-38.683	-9.7316

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47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4320	N307	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4321	N308	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4336	N309	-38.683	-9.7316
47	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4515	N312	-38.683	-9.7316
48	<i>Cnemidophorus ocellifer</i>	Paulo Afonso	BA	UFPB	A124	N458	-38.1172	-9.5131
49	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A129	N459	-37.877	-9.7567
49	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A135	N460	-37.877	-9.7567
49	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A144	N463	-37.877	-9.7567
49	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A145	N464	-37.877	-9.7567
49	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A67	N451	-37.877	-9.7567
49	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	FSCHUFPB291	N392	-37.877	-9.7567
50	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A117	N457	-37.744	-9.8168
50	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A148	N465	-37.744	-9.8168
50	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A149	N466	-37.744	-9.8168
50	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A151	N468	-37.744	-9.8168
50	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A73	N453	-37.744	-9.8168
50	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A89	N455	-37.744	-9.8168
50	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A93	N456	-37.744	-9.8168
51	<i>Cnemidophorus ocellifer</i>	Olho d'água das Flores	AL	UFAL	MUFAL9161	N538	-37.2954	-9.6005
52	<i>Cnemidophorus ocellifer</i>	Traipu	AL	UFAL	MUFAL10106	N539	-36.9679	-9.8978
52	<i>Cnemidophorus ocellifer</i>	Traipu	AL	UFAL	MUFAL10190	N540	-36.9679	-9.8978
52	<i>Cnemidophorus ocellifer</i>	Traipu	AL	UFAL	MUFAL10191	N541	-36.9679	-9.8978
53	<i>Cnemidophorus ocellifer</i>	Nossa Senhora da Glória	SE	UFPB	L133	N495	-37.354	-10.205
53	<i>Cnemidophorus ocellifer</i>	Nossa Senhora da Glória	SE	UFPB	L136	N496	-37.354	-10.205
53	<i>Cnemidophorus ocellifer</i>	Nossa Senhora da Glória	SE	UFPB	L149	N497	-37.354	-10.205
53	<i>Cnemidophorus ocellifer</i>	Nossa Senhora da Glória	SE	UFPB	L150	N498	-37.354	-10.205
54	<i>Cnemidophorus ocellifer</i>	Piaçabuçu	AL	UFRN	EFO264	N273	-36.4905	-10.3746
54	<i>Cnemidophorus ocellifer</i>	Piaçabuçu	AL	UFRN	EFO265	N274	-36.4905	-10.3746
55	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12567	N723	-37.072	-10.788
55	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12569	N724	-37.072	-10.788
55	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12570	N725	-37.072	-10.788
55	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12571	N726	-37.072	-10.788
55	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12572	N727	-37.072	-10.788
55	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12573	N728	-37.072	-10.788

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
55	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12574	N729	-37.072	-10.788
56	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO269	N277	-37.568	-11.857
56	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO270	N278	-37.568	-11.857
56	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO271	N279	-37.568	-11.857
56	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO272	N280	-37.568	-11.857
56	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO273	N281	-37.568	-11.857
57	<i>Cnemidophorus ocellifer</i>	Massarandupió	BA	UFPB	A7	N568	-37.8384	-12.3195
58	<i>Cnemidophorus ocellifer</i>	Itacimirim	BA	USP	MRT12553	N717	-38.0764	-12.6431
58	<i>Cnemidophorus ocellifer</i>	Itacimirim	BA	USP	MRT12554	N718	-38.0764	-12.6431
58	<i>Cnemidophorus ocellifer</i>	Itacimirim	BA	USP	MRT12555	N719	-38.0764	-12.6431
59	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	A2	N563	-38.271	-12.862
59	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	CHECOA2483	N553	-38.271	-12.862
59	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	CHECOA2484	N554	-38.271	-12.862
59	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	CHECOA2486	N555	-38.271	-12.862
59	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	CHECOA2488	N556	-38.271	-12.862
60	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO251	N260	-38.773	-10.974
60	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO252	N261	-38.773	-10.974
60	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO253	N262	-38.773	-10.974
60	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO254	N263	-38.773	-10.974
60	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO255	N264	-38.773	-10.974
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO235	N244	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO237	N246	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO239	N248	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO240	N249	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO241	N250	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO243	N252	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO244	N253	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO245	N254	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO246	N255	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO247	N256	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO248	N257	-39.92	-10.704
61	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO249	N258	-39.92	-10.704
62	<i>Cnemidophorus ocellifer</i>	Campo Formoso	BA	USP	LG1344	N581	-40.3000	-10.5000
63	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO228	N237	-40.147	-11.703

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
63	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO229	N238	-40.147	-11.703
63	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO230	N239	-40.147	-11.703
63	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO231	N240	-40.147	-11.703
63	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO232	N241	-40.147	-11.703
63	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO233	N242	-40.147	-11.703
64	<i>Cnemidophorus ocellifer</i>	Itaberaba	BA	UFRN	EFO198	N212	-40.225	-12.521
64	<i>Cnemidophorus ocellifer</i>	Itaberaba	BA	UFRN	EFO199	N213	-40.225	-12.521
64	<i>Cnemidophorus ocellifer</i>	Itaberaba	BA	UFRN	EFO200	N214	-40.225	-12.521
64	<i>Cnemidophorus ocellifer</i>	Itaberaba	BA	UFRN	EFO203	N217	-40.225	-12.521
65	<i>Cnemidophorus</i> sp.	Lençóis	BA	USP	MTR19916	N761	-41.364	-12.546
65	<i>Cnemidophorus</i> sp.	Lençóis	BA	USP	MTR19917	N762	-41.364	-12.546
65	<i>Cnemidophorus</i> sp.	Lençóis	BA	USP	MTR19918	N763	-41.364	-12.546
65	<i>Cnemidophorus</i> sp.	Lençóis	BA	USP	MTR19989	N764	-41.364	-12.546
66	<i>Cnemidophorus ocellifer</i>	Seabra	BA	UFRN	EFO210	N223	-41.7611	-12.4280
67	<i>Cnemidophorus ocellifer</i>	Morro do Chapéu	BA	USP	LG488	N580	-41.2000	-11.5833
67	<i>Cnemidophorus ocellifer</i>	Morro do Chapéu	BA	USP	MTR20020	N765	-41.2000	-11.5833
67	<i>Cnemidophorus ocellifer</i>	Morro do Chapéu	BA	USP	MTR20021	N766	-41.2000	-11.5833
67	<i>Cnemidophorus ocellifer</i>	Morro do Chapéu	BA	USP	MTR20024	N767	-41.2000	-11.5833
68	<i>Cnemidophorus ocellifer</i>	Gentio do Ouro	BA	USP	MRT11350	N697	-42.5419	-11.4817
68	<i>Cnemidophorus ocellifer</i>	Gentio do Ouro	BA	USP	MRT11356	N698	-42.5419	-11.4817
68	<i>Cnemidophorus ocellifer</i>	Gentio do Ouro	BA	USP	MRT3265	N631	-42.5419	-11.4817
68	<i>Cnemidophorus ocellifer</i>	Gentio do Ouro	BA	USP	MRT3266	N632	-42.5419	-11.4817
69	<i>Cnemidophorus ocellifer</i>	Santo Inácio	BA	USP	MTR11127	N659	-42.7214	-11.1111
69	<i>Cnemidophorus ocellifer</i>	Santo Inácio	BA	USP	MTR11128	N660	-42.7214	-11.1111
69	<i>Cnemidophorus ocellifer</i>	Santo Inácio	BA	USP	MTR11201	N661	-42.7214	-11.1111
69	<i>Cnemidophorus ocellifer</i>	Santo Inácio	BA	USP	MRT2982	N628	-42.7214	-11.1111
69	<i>Cnemidophorus</i> sp.	Santo Inácio	BA	USP	MRT3107	N629	-42.7214	-11.1111
69	<i>Cnemidophorus</i> sp.	Santo Inácio	BA	USP	MRT3111	N630	-42.7214	-11.1111
69	<i>Cnemidophorus ocellifer</i>	Santo Inácio	BA	USP	MRT3275	N633	-42.7214	-11.1111
70	<i>Cnemidophorus ocellifer</i>	Barra	BA	USP	MRT11296	N680	-43.2525	-11.1106
70	<i>Cnemidophorus ocellifer</i>	Barra	BA	USP	MRT11308	N688	-43.2525	-11.1106
70	<i>Cnemidophorus ocellifer</i>	Barra	BA	USP	MRT11309	N689	-43.2525	-11.1106
71	<i>Cnemidophorus ocellifer</i>	Buritirama	BA	USP	MRT11300	N681	-43.4806	-10.9589
71	<i>Cnemidophorus ocellifer</i>	Buritirama	BA	USP	MRT11301	N682	-43.4806	-10.9589

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
71	<i>Cnemidophorus ocellifer</i>	Buritirama	BA	USP	MRT11302	N683	-43.4806	-10.9589
71	<i>Cnemidophorus ocellifer</i>	Buritirama	BA	USP	MRT11304	N684	-43.4806	-10.9589
71	<i>Cnemidophorus ocellifer</i>	Buritirama	BA	USP	MRT11305	N685	-43.4806	-10.9589
71	<i>Cnemidophorus ocellifer</i>	Buritirama	BA	USP	MRT11307	N687	-43.4806	-10.9589
72	<i>Cnemidophorus ocellifer</i>	Ibotirama	BA	UFRN	EFO215	N228	-43.2048	-12.1774
72	<i>Cnemidophorus ocellifer</i>	Ibotirama	BA	UFRN	EFO216	N229	-43.2048	-12.1774
72	<i>Cnemidophorus ocellifer</i>	Ibotirama	BA	UFRN	EFO219	N232	-43.2048	-12.1774
72	<i>Cnemidophorus ocellifer</i>	Ibotirama	BA	UFRN	EFO220	N233	-43.2048	-12.1774
72	<i>Cnemidophorus ocellifer</i>	Ibotirama	BA	UFRN	EFO221	N234	-43.2048	-12.1774
72	<i>Cnemidophorus ocellifer</i>	Ibotirama	BA	UFRN	EFO223	N236	-43.2048	-12.1774
73	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	São Desidério	BA	USP	MTR17857	N750	-44.9667	-12.3500
73	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	São Desidério	BA	USP	MTR17858	N751	-44.9667	-12.3500
73	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	São Desidério	BA	USP	MTR17859	N752	-44.9667	-12.3500
73	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	São Desidério	BA	USP	MTR17890	N753	-44.9667	-12.3500
73	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	São Desidério	BA	USP	MTR17891	N754	-44.9667	-12.3500
73	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	São Desidério	BA	USP	MTR17892	N755	-44.9667	-12.3500
73	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	São Desidério	BA	USP	MTR17893	N756	-44.9667	-12.3500
73	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	São Desidério	BA	USP	MTR17894	N757	-44.9667	-12.3500
73	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	São Desidério	BA	USP	MTR17895	N758	-44.9667	-12.3500
74	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	PARNA Cavernas do Peruaçu	MG	USP	MTJ11	N771	-44.3041	-15.1546
74	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	PARNA Cavernas do Peruaçu	MG	USP	MTJ12	N772	-44.3041	-15.1546
74	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	PARNA Cavernas do Peruaçu	MG	USP	MTJ13	N773	-44.3041	-15.1546
74	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	PARNA Cavernas do Peruaçu	MG	USP	MTJ14	N774	-44.3041	-15.1546
74	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	PARNA Cavernas do Peruaçu	MG	USP	MTJ25	N775	-44.3041	-15.1546
74	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	PARNA Cavernas do Peruaçu	MG	USP	MTJ9	N770	-44.3041	-15.1546
75	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Montezuma	MG	USP	MTR16539	N744	-42.4722	-15.1803
76	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Condeuba	BA	USP	MTR16453	N741	-41.9496	-14.9336
76	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Condeuba	BA	USP	MTR16487	N742	-41.9496	-14.9336
76	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Condeuba	BA	USP	MTR16538	N743	-41.9496	-14.9336
77	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Grão Mogol	MG	USP	MTR16557	N745	-42.8627	-16.2318
77	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Grão Mogol	MG	USP	MTR16558	N746	-42.8627	-16.2318
78	<i>Cnemidophorus</i> cf. <i>ocellifer</i>	Brasilândia de Minas	MG	UFV	MRM344	N537	-46.0094	-17.0097

\*outgroup; Institution abbreviations: Universidade de Brasília (UnB), Universidade de São Paulo (USP), Universidade Católica do Salvador (UCSAL), Universidade Federal da Paraíba (UFPB), Universidade Federal do Rio Grande do Norte (UFRN), Universidade Federal de Alagoas

(UFAL), Universidade Federal de Viçosa (UFV), and Universidade Federal do Ceará (UFC); Locality abbreviations: National Park (PARNA), Ecological Station (EE), and National Forest (FLONA); State abbreviations: Alagoas (AL), Bahia (BA), Ceará (CE), Maranhão (MA), Minas Gerais (MG), Paraíba (PB), Pernambuco (PE), Piauí (PI), Rio Grande do Norte (RN), and Sergipe (SE).

Table S2. Primers used for amplification and sequencing of the five loci used in this study. Each primer presents the source of origin and the annealing temperature (T) in degrees Celsius (°C).

<b>Locus</b>	<b>Name</b>	<b>Primer</b>	<b>Source</b>	<b>T</b>
12S	12Sa	5'- AAA CTG GGA TTA GAT ACC CCA CTA T - 3'	Lilian Giugliano*	50
	12Sb	5'- GAG GGT GAC GGG CGG TGT GT -3'	Lilian Giugliano*	59.8
RP40	RP40f	5'- ATG TGG TGG ATG YTG GCT CGT -3'	Tod Reeder*	55.4
	RP40r	5'- GCT TCT CAG CWG CRG CCT GC -3'	Tod Reeder*	57
	RP40-F1	5'- GCC TGC TCC TCC TTC TCA ATC TGC -3'	this study	56.6
	RP40-R1	5'- GCT CGT GAG GTC CTG CGT ATG CGT -3'	this study	60
ATPSB	ATPSBf	5'- TAC CAT GAR ATG ATT GAA TCT GGR GTC -3'	Tod Reeder*	52.8
	ATPSBr	5'- CKA GCA CGA GCA CCT GGT GGG TCR TT -3'	Tod Reeder*	61.7
	ATPSB-F1	5'- TTC TGG GAA CTT CAG AAT -3'	this study	42.7
	ATPSB-R1	5'- CTT GAG CAA CAY TGG TCC -3'	this study	47.4
NKTR	NKTRf19	5'- GAT GAC ATG GAG ATY TGY ACT CC -3'	Tod Reeder*	50.1
	NKTRr18	5'- CTY CTD GAY CGA CTT CTT GAG TGA CT -3'	Tod Reeder*	53.3
	NKTR-F1	5'- CTC CAG TAA GTC TGC GGG TG -3'	this study	52.5
	NKTR-R1	5'- ACT CCT CGA TCG RCT GTG GC -3'	this study	55.5
R35	R35f	5'- CCA GTG AGC ATG ATA TGG G -3'	Frank Burbrink	47.8
	R35r	5'- GTT TCT GAC CAA AYT CCA CAG T -3'	Frank Burbrink	49.6

\*personal communication.

Table S3. Analyses performed in BEAST program. For each analysis is presented the locus used, number of sequences (N), substitution model estimated by jModelTest program, and settings for molecular clock, mutation rate, tree prior, chain size (MCMC) and sampling frequency (Freq).

Analysis	Locus	N	Model	Main BEAST parameters				
				Clock	Rate	Tree prior	MCMC	Freq
Gene tree	12S	137	HKY+I+G	lognormal	$1 \times 10^{-8}$	Coalescent: CS	$2 \times 10^7$	$2 \times 10^3$
Gene tree	ATPSB	126	K80	strict	1.0	Coalescent: CS	$2 \times 10^7$	$2 \times 10^3$
Gene tree	NKTR	115	TrN+I	strict	1.0	Coalescent: CS	$2 \times 10^7$	$2 \times 10^3$
Gene tree	R35	134	JC	strict	1.0	Coalescent: CS	$2 \times 10^7$	$2 \times 10^3$
Gene tree	RP40	132	JC	strict	1.0	Coalescent: CS	$2 \times 10^7$	$2 \times 10^3$
Substitution rate estimation	12S	‡62	GTR+I+G	lognormal	-	Speciation: YP	$1 \times 10^8$	$1 \times 10^4$
Species tree and divergence dating	12S	137	HKY+I+G	lognormal	§ $5.11 \times 10^{-3}$			
	ATPSB	*252	K80+I	strict	$1 \times 10^{-3}$			
	NKTR	*230	TrN+I	strict	$1 \times 10^{-3}$	Speciation: BDP	$5 \times 10^8$	$5 \times 10^4$
	R35	*268	K80	strict	$1 \times 10^{-3}$			
	RP40	*264	JC	strict	$1 \times 10^{-3}$			
Bayesian Skyline - Northeast	12S	111	HKY+I	lognormal	$5.11 \times 10^{-9}$	Coalescent: BS	$5 \times 10^7$	$5 \times 10^3$
Bayesian Skyline - Southwest	12S	26	K80+I	lognormal	$5.11 \times 10^{-9}$	Coalescent: BS	$5 \times 10^7$	$5 \times 10^3$
Center of origin - Northeast	12S	111	HKY+I	lognormal	$5.11 \times 10^{-3}$	Coalescent: CS	$5 \times 10^7$	$5 \times 10^3$
Center of origin - Northeast	ATPSB	*206	K80+I	strict	† $5.11 \times 10^{-4}$	Coalescent: CS	$5 \times 10^7$	$5 \times 10^3$
Center of origin - Northeast	NKTR	*190	TrN+I	strict	† $9.71 \times 10^{-4}$	Coalescent: CS	$5 \times 10^7$	$5 \times 10^3$
Center of origin - Northeast	R35	*220	JC	strict	† $1.89 \times 10^{-4}$	Coalescent: CS	$1 \times 10^8$	$1 \times 10^4$
Center of origin - Northeast	RP40	*216	JC	strict	† $1.51 \times 10^{-4}$	Coalescent: CS	$1.5 \times 10^8$	$1.5 \times 10^4$

‡samples used in estimating the 12S substitution rate are presented in Table S4; §mutation rate for the mitochondrial fragment obtained by substitution rate estimation; \*phased sequences; †values obtained from \*BEAST estimation based on mutation rate for the mitochondrial fragment ( $5.11 \times 10^{-3}$  substitutions/site/Ma); tree prior abbreviations: Constant Size (CS), Yule Process (YP), Birth-Death Process (BDP), and Bayesian Skyline (BS).



Table S4. Species used in estimating the 12S substitution rate for Teiidae.

<b>Species</b>	<b>Subfamily</b>	<b>Source</b>	<b>Code</b>
<i>Ameiva aggerescusans</i>	Teiinae	GenBank	KF742697
<i>Ameiva ameiva</i>	Teiinae	GenBank	AY359473
<i>Ameiva auberi</i>	Teiinae	GenBank	AY046424
<i>Ameiva bifrontata</i>	Teiinae	GenBank	AY046454
<i>Ameiva chrysoleama</i>	Teiinae	GenBank	AY046425
<i>Ameiva concolor</i>	Teiinae	GenBank	KF742691
<i>Ameiva corax</i>	Teiinae	GenBank	AY359477
<i>Ameiva dorsalis</i>	Teiinae	GenBank	AY359478
<i>Ameiva erythrocephala</i>	Teiinae	GenBank	AY359479
<i>Ameiva exsul</i>	Teiinae	GenBank	AY359480
<i>Ameiva festiva</i>	Teiinae	GenBank	AY359481
<i>Ameiva fuscata</i>	Teiinae	GenBank	AY359482
<i>Ameiva griswold</i>	Teiinae	GenBank	AY359483
<i>Ameiva jacuba</i>	Teiinae	GenBank	JQ762441
<i>Ameiva lineotata</i>	Teiinae	GenBank	AY292295
<i>Ameiva maynardi</i>	Teiinae	GenBank	AY359486
<i>Ameiva nodam</i>	Teiinae	GenBank	KF742687
<i>Ameiva parecis</i>	Teiinae	GenBank	JQ762438
<i>Ameiva plei</i>	Teiinae	GenBank	AY359487
<i>Ameiva pluvianotata</i>	Teiinae	GenBank	AY359488
<i>Ameiva quadrilineata</i>	Teiinae	GenBank	AY046426
<i>Ameiva taenura</i>	Teiinae	GenBank	AY292294
<i>Ameiva undulata</i>	Teiinae	GenBank	AY046427
<i>Ameiva wetmorei</i>	Teiinae	GenBank	AY359492
<i>Aspidosceis costatus</i>	Teiinae	GenBank	AY046429
<i>Aspidosceis hyperythrus</i>	Teiinae	GenBank	AY046435
<i>Aspidosceis inornatus</i>	Teiinae	GenBank	AY046436
<i>Aspidoscelis burti</i>	Teiinae	GenBank	AY046428
<i>Aspidoscelis deppei</i>	Teiinae	GenBank	AY046431
<i>Aspidoscelis gularis</i>	Teiinae	GenBank	AY046433
<i>Aspidoscelis sexlineatus</i>	Teiinae	GenBank	AY046444
<i>Aspidoscelis tigris</i>	Teiinae	GenBank	AY046452
<i>Callopistes flavipunctatus</i>	Tupinambinae	GenBank	EF029873
<i>Callopistes maculatus</i>	Tupinambinae	GenBank	EF029874
<i>Cercosaura ocellata*</i>	Cercosaurinae	GenBank	AF420677
<i>Cnemidophorus arenivagus</i>	Teiinae	GenBank	AY046441
<i>Cnemidophorus gramivagus</i>	Teiinae	GenBank	AY046432
<i>Cnemidophorus lacertoides</i>	Teiinae	GenBank	AY046437
<i>Cnemidophorus lemniscatus lemniscatus</i>	Teiinae	GenBank	AY046438
<i>Cnemidophorus lemniscatus splendidus</i>	Teiinae	GenBank	AY046440
<i>Cnemidophorus longicaudus</i>	Teiinae	GenBank	AY046439
<i>Cnemidophorus ocellifer</i>	Teiinae	GenBank	AF420706
<i>Cnemidophorus ocellifer</i>	Teiinae	this study	N100

<b>Species</b>	<b>Subfamily</b>	<b>Source</b>	<b>Code</b>
<i>Cnemidophorus ocellifer</i>	Teiinae	this study	N537
<i>Cnemidophorus ruatanus</i>	Teiinae	GenBank	KF667262
<i>Cnemidophorus vanzoi</i>	Teiinae	GenBank	DQ168984
<i>Crocodylus amazonicus</i>	Tupinambinae	GenBank	EF029876
<i>Crocodylus amazonicus</i>	Tupinambinae	GenBank	EF029877
<i>Dicrodon guttulatum</i>	Teiinae	GenBank	AY046453
<i>Dracaena guianensis</i>	Tupinambinae	GenBank	EF029878
<i>Dracaena guianensis</i>	Tupinambinae	GenBank	EF029879
<i>Kentropyx altamazonica</i>	Teiinae	GenBank	AY046455
<i>Kentropyx borkiana</i>	Teiinae	GenBank	AY046457
<i>Kentropyx calcarata</i>	Teiinae	GenBank	AY046458
<i>Kentropyx paulensis</i>	Teiinae	GenBank	EU345185
<i>Kentropyx pelviceps</i>	Teiinae	GenBank	AY046459
<i>Kentropyx striata</i>	Teiinae	GenBank	AY046460
<i>Kentropyx vanzoi</i>	Teiinae	GenBank	EU345188
<i>Kentropyx viridistriga</i>	Teiinae	GenBank	EU345186
<i>Teius teyou</i>	Teiinae	GenBank	AY046461
<i>Tupinambis teguixim</i>	Tupinambinae	GenBank	AY046422
<i>Tupinambis teguixim</i>	Tupinambinae	GenBank	AY359490

\*outgroup.

Table S5. Parameters and prior distributions used to test alternative scenarios for diversification of the Northeast and Southwest lineages under ABC approach.

Parameter	Code	Prior distribution	Prior values		Source
Population size	NE	unif (min, max)	4,000,000	6,500,000	IMa2
	SW	unif (min, max)	4,700,000	8,500,000	IMa2
Migration rate	$m_{NE\_SW}$	unif (min, max)	0.4	1.6	IMa2
	$m_{SW\_NE}$	unif (min, max)	0.04	1.6	IMa2
Divergence time	$T_1$	unif (min, max)	3,250,000	7,500,000	IMa2
	$T_1$	unif (min, max)	580,000	1,550,000	*BEASTt
Population expansion and/or recent migration	$T_2$	unif (min, max)	100,000	250,000	Skyline Plot
Ancestral population	$NE_{Anc}$	unif (min, max)	NE/2	NE/1000	Skyline Plot
	$SW_{Anc}$	unif (min, max)	SW/2	SW/100	Skyline Plot
Founder population	$NE_F$	unif (min, max)	100	1,000	Arbitrary
Mutation rate	ATPSB.rate	norm (mean, SD)	1.02E-09	2.00E-10	*BEAST
	RP40.rate	norm (mean, SD)	3.00E-10	5.00E-11	*BEAST
	R35.rate	norm (mean, SD)	3.78E-10	8.00E-11	*BEAST
	NKTR.rate	norm (mean, SD)	1.94E-09	5.00E-10	*BEAST
	mt.rate	norm (mean, SD)	1.02E-08	9.00E-10	BEAST

Population size: Northeast (NE) and Southwest (SW) lineages; Migration rate: population migration rate at which the individuals of Northeast are supplanted by individuals from Southwest ( $m_{NE\_SW}$ ) and the reverse ( $m_{SW\_NE}$ ); Prior distribution: uniform (unif) distribution and its minimum (min) and maximum (max) values, and normal distribution and its mean and standard deviation (SD).

Table S6. Samples of *Cnemidophorus* used in this study (subset of 137 samples). For each sample is presented map code number (see Fig. 1), collection locality, state, laboratory code number, populations found by the GENELAND and STRUCTURE analysis, and mtDNA and nuDNA haplotypes (see Fig. 3). Number 2 between parentheses indicates homozygous individuals.

Map code	Locality	State	Lab code	Population	Haplotypes				
					12S	NKTR	ATPSB	R35	RP40
1	Alcântara	MA	N658	Northeast	H79	H1, H22	H5 (2)	H2 (2)	H1 (2)
2	Joaquim Pires	PI	N100	Northeast	H1	H1 (2)	H1, H2	H1 (2)	H1 (2)
3	Batalha	PI	N105	Northeast	H2	H2, H3	*	H1, H2	H1, H2
3	Batalha	PI	N108	Northeast	H3	H3, H4	H2 (2)	H1, H2	H1 (2)
4	Nossa Senhora de Nazaré	PI	N110	Northeast	H2	H3 (2)	H3 (2)	H1, H2	H1 (2)
4	Nossa Senhora de Nazaré	PI	N111	Northeast	H4	*	H3, H4	H1, H2	H1 (2)
5	PARNA Sete Cidades	PI	N16	Northeast	H1	H1, H11	H2 (2)	H1, H2	*
5	PARNA Sete Cidades	PI	N17	Northeast	H1	H1, H13	H5 (2)	H1 (2)	H1, H2
5	PARNA Sete Cidades	PI	N21	Northeast	H25	H1 (2)	H5 (2)	H1 (2)	H1, H2
5	PARNA Sete Cidades	PI	N22	Northeast	H1	H1 (2)	H5 (2)	H1 (2)	H2 (2)
6	São João da Fronteira	PI	N113	Northeast	H5	H1 (2)	H2, H5	H1 (2)	H1 (2)
6	São João da Fronteira	PI	N117	Northeast	H6	H1 (2)	H2, H5	H2 (2)	H1 (2)
6	São João da Fronteira	PI	N118	Northeast	H7	H1, H3	H6 (2)	H1 (2)	H1, H2
7	Viçosa do Ceará	CE	N526	Northeast	H5	H1 (2)	H2, H5	H1 (2)	H2 (2)
8	Jericoacoara	CE	N776	Northeast	H102	*	H60 (2)	H1 (2)	H1 (2)
9	Santa Quitéria	CE	N394	Northeast	H46	H1 (2)	H28 (2)	H1 (2)	H1 (2)
9	Santa Quitéria	CE	N406	Northeast	H47	H1, H3	H5 (2)	H1 (2)	H1 (2)
10	São Gonçalo do Amarante	CE	N84	Northeast	H24	H1 (2)	H2, H5	H1, H2	H1 (2)
10	São Gonçalo do Amarante	CE	N88	Northeast	H93	H1 (2)	H1, H2	H1 (2)	H1, H6
11	Caucaia	CE	N528	Northeast	H24	*	H1, H2	H12, H1	H1, H3
11	Caucaia	CE	N529	Northeast	H62	H39, H40	*	H11, H12	H2 (2)
12	Pacajus	CE	N521	Northeast	H5	H1 (2)	H7 (2)	H11, H1	H1 (2)
13	Galinhos	RN	N502	Northeast	H22	H1 (2)	H7 (2)	H1 (2)	H2 (2)
13	Galinhos	RN	N503	Northeast	H60	H1 (2)	*	H1 (2)	H2 (2)

Map code	Locality	State	Lab code	Population	Haplotypes				
					12S	NKTR	ATPSB	R35	RP40
13	Galinhos	RN	N506	Northeast	H61	H1 (2)	H7 (2)	H1 (2)	H1 (2)
14	João Câmara	RN	N334	Northeast	H45	H1 (2)	H7 (2)	H1 (2)	H2 (2)
15	Barra do Cunhau	RN	N434	Northeast	H5	H1 (2)	H7 (2)	H9, H1	H2 (2)
16	Rio Tinto	PB	N389	Northeast	H5	H1 (2)	H27 (2)	H1 (2)	H2 (2)
17	João Pessoa	PB	N408	Northeast	H5	H1, H3	H7 (2)	H1 (2)	H1, H2
18	Cruz do Espírito Santo	PB	N501	Northeast	H59	H1 (2)	H7 (2)	H1 (2)	H1, H2
19	Caruaru	PE	N206	Northeast	H23	H1, H22	H10, H11	H1 (2)	H1, H2
19	Caruaru	PE	N208	Northeast	H24	H1 (2)	H12, H13	*	H1, H2
20	Cabaceiras	PB	N415	Northeast	H48	H1, H35	H7 (2)	H1 (2)	H1, H2
21	Caicó	RN	N47	Northeast	H5	H1 (2)	H7 (2)	H10, H1	H2 (2)
21	Caicó	RN	N48	Northeast	H55	H36, H37	H7 (2)	H1 (2)	H2 (2)
22	Vista Serrana	PB	N55	Northeast	H5	H42, H43	H7 (2)	H1 (2)	H1, H2
23	Itaporanga	PB	N23	Northeast	H5	H1 (2)	H7 (2)	H1 (2)	H2 (2)
24	Serra Talhada	PE	N490	Northeast	H57	H1 (2)	H1, H10	H1 (2)	H2 (2)
25	Salgueiro	PE	N132	Northeast	H8	H1, H5	H7 (2)	H1 (2)	H1, H2
26	FLONA Chapada do Araripe	CE	N39	Northeast	H5	H1, H22	H1, H5	H1 (2)	H1 (2)
27	Nova Olinda	CE	N708	Northeast	H92	H1 (2)	H50 (2)	H1 (2)	H1, H2
27	Nova Olinda	CE	N709	Northeast	H93	H1 (2)	H51, H52	H1 (2)	H1 (2)
28	Mineirolândia	CE	N62	Northeast	H74	H1 (2)	H2, H5	H15, H1	H1, H6
29	Tauá	CE	N74	Northeast	H95	H1, H22	H5 (2)	H20, H1	H1, H2
29	Tauá	CE	N75	Northeast	H97	*	H28 (2)	H1 (2)	H1 (2)
30	Trindade	PE	N477	Northeast	H17	H1 (2)	*	H2 (2)	H1, H6
31	Nascente	PE	N480	Northeast	H56	H1 (2)	H1, H5	H1 (2)	H1, H3
32	Picos	PI	N138	Northeast	H9	H1 (2)	H5 (2)	H1 (2)	H1 (2)
32	Picos	PI	N141	Northeast	H9	H1 (2)	H1(2)	H2 (2)	*
33	Simplício Mendes	PI	N146	Northeast	H10	H1, H6	H5 (2)	H1 (2)	H1, H2
33	Simplício Mendes	PI	N150	Northeast	H11	H6, H7	H5 (2)	H1 (2)	H1, H3
33	Simplício Mendes	PI	N153	Northeast	H12	H7, H8	H1, H5	H2 (2)	H1, H2

Map code	Locality	State	Lab code	Population	Haplotypes				
					12S	NKTR	ATPSB	R35	RP40
34	Capitão Gervásio de Oliveira	PI	N582	Northeast	H70	H1, H6	H38, H39	H1 (2)	H1, H10
34	Capitão Gervásio de Oliveira	PI	N585	Northeast	H71	H1, H6	H5 (2)	H1, H2	H1, H3
34	Capitão Gervásio de Oliveira	PI	N597	Northeast	H72	H1, H6	H5 (2)	H5 (2)	H1, H3
34	Capitão Gervásio de Oliveira	PI	N598	Northeast	H73	H1, H6	H5 (2)	H1, H2	H1, H6
34	Capitão Gervásio de Oliveira	PI	N600	Northeast	H73	H1, H6	*	H1, H2	H1, H3
35	Coronel José Dias	PI	N156	Northeast	H13	H9, H10	H1, H5	H1 (2)	H1 (2)
35	Coronel José Dias	PI	N161	Northeast	H14	H1, H12	H5 (2)	H1 (2)	H1 (2)
36	PARNA Serra da Capivara	PI	N313	Northeast	H42	*	H5 (2)	H2 (2)	H1, H2
36	PARNA Serra da Capivara	PI	N317	Northeast	H43	H32 (2)	H5 (2)	H1 (2)	H3 (2)
36	PARNA Serra da Capivara	PI	N320	Northeast	H43	H10, H32	H21, H26	H1, H2	H3 (2)
36	PARNA Serra da Capivara	PI	N321	Northeast	H44	H6, H33	H1, H5	H1, H2	H1, H3
36	PARNA Serra da Capivara	PI	N330	Northeast	H12	H32, H34	H1, H5	H1, H2	H1 (2)
37	Rio Grande do Piauí	PI	N475	Northeast	H54	H14, H15	H1, H5	H2 (2)	H1 (2)
38	Uruçuí-Una	PI	N624	Southwest	H75	H45, H46	*	H2 (2)	H6, H11
38	Uruçuí-Una	PI	N625	Southwest	H76	H47 (2)	H40, H41	*	H12, H13
39	Caracol	PI	N171	Northeast	H15	*	H5 (2)	H2 (2)	H1, H3
40	Remanso	BA	N177	Northeast	H13	H14, H15	H7 (2)	H1, H2	*
40	Remanso	BA	N178	Northeast	H16	*	H8 (2)	H1, H2	H1 (2)
41	Serra do Lajedo	BA	N707	Northeast	H91	H14, H55	H1, H5	H1, H2	H1, H6
42	Atoleiro	BA	N705	Northeast	H90	H1, H54	H5 (2)	H1, H2	H1 (2)
43	Alagoado	BA	N670	Southwest	H83	*	H42, H43	H1 (2)	H10 (2)
43	Alagoado	BA	N676	Southwest	H21	H49, H50	H42, H43	H17, H1	*
43	Alagoado	BA	N678	Southwest	H84	H51 (2)	*	H17, H1	H10 (2)
44	Casa Nova	BA	N179	Northeast	H17	H1, H8	H5, H9	H2 (2)	H1, H3
44	Casa Nova	BA	N180	Northeast	H18	H16, H17	H1, H10	H1, H2	H1 (2)
44	Casa Nova	BA	N181	Northeast	H19	H18, H19	*	H1 (2)	H1 (2)
44	Casa Nova	BA	N185	Northeast	H20	*	H5 (2)	H1, H2	H1 (2)
44	Casa Nova	BA	N188	Northeast	H21	H6, H20	H1, H5	H1, H2	H1 (2)

Map code	Locality	State	Lab code	Population	Haplotypes				
					12S	NKTR	ATPSB	R35	RP40
45	Petrolina	PE	N652	Northeast	H77	H48 (2)	H1, H5	H1, H2	H1, H3
45	Petrolina	PE	N657	Northeast	H78	*	H5 (2)	H2 (2)	H3 (2)
45	Petrolina	PE	N666	Northeast	H81	*	H5 (2)	H16, H1	H1 (2)
45	Petrolina	PE	N667	Northeast	H82	H1, H6	H5 (2)	H1, H2	H3 (2)
46	Belém do São Francisco	PE	N192	Northeast	H5	H1, H21	H7 (2)	H1 (2)	H2 (2)
46	Belém do São Francisco	PE	N194	Northeast	H22	H1 (2)	H1, H5	H1, H2	H1, H2
46	Belém do São Francisco	PE	N196	Northeast	H1	H1, H21	H7 (2)	H1 (2)	H1, H2
47	EE Raso da Catarina	BA	N299	Northeast	H40	*	H14 (2)	H2 (2)	H1 (2)
47	EE Raso da Catarina	BA	N301	Northeast	H41	H1 (2)	H5, H10	H8, H2	H1, H2
47	EE Raso da Catarina	BA	N309	Northeast	H34	H1, H31	H14 (2)	H2 (2)	H1 (2)
48	Paulo Afonso	BA	N458	Northeast	H38	H1 (2)	H5 (2)	H2 (2)	H1 (2)
49	Canindé de São Francisco	SE	N459	Northeast	H51	H1 (2)	H5 (2)	H2 (2)	H1 (2)
49	Canindé de São Francisco	SE	N460	Northeast	H52	H1 (2)	*	H2 (2)	H1 (2)
49	Canindé de São Francisco	SE	N463	Northeast	H53	H1 (2)	H5 (2)	H2 (2)	H1 (2)
50	Poço Redondo	SE	N455	Northeast	H49	H1 (2)	H29 (2)	H2 (2)	H1 (2)
50	Poço Redondo	SE	N457	Northeast	H50	*	H5, H10	H2 (2)	H1 (2)
51	Olho d'água das Flores	AL	N538	Northeast	H64	*	H14 (2)	H7 (2)	H2 (2)
52	Traipu	AL	N541	Northeast	H65	H1 (2)	H33, H34	H2 (2)	H2 (2)
53	Nossa Senhora da Glória	SE	N495	Northeast	H34	H22, H38	H14 (2)	H2 (2)	H7 (2)
53	Nossa Senhora da Glória	SE	N497	Northeast	H58	H1 (2)	H30, H31	H2 (2)	H1 (2)
54	Piaçabuçu	AL	N273	Northeast	H38	H30 (2)	H25 (2)	H7 (2)	H7 (2)
55	Santo Amaro das Brotas	SE	N724	Northeast	H94	H1, H21	*	H2 (2)	H1 (2)
56	Conde	BA	N277	Northeast	H39	H1 (2)	H10, H24	H2 (2)	H1 (2)
56	Conde	BA	N280	Northeast	H39	H1, H30	H5, H24	H2 (2)	H1 (2)
57	Massarandupió	BA	N568	Northeast	H67	*	H5 (2)	H2 (2)	H1 (2)
58	Itacimirim	BA	N719	Northeast	H36	H1, H22	H14 (2)	H2 (2)	H1 (2)
59	Busca Vida	BA	N563	Northeast	H66	H1 (2)	H14 (2)	H2 (2)	H1, H2
60	Tucano	BA	N260	Northeast	H36	*	H5, H24	H2 (2)	H1 (2)

Map code	Locality	State	Lab code	Population	Haplotypes				
					12S	NKTR	ATPSB	R35	RP40
60	Tucano	BA	N263	Northeast	H37	H1, H22	H10, H21	H2 (2)	H1 (2)
61	Itiúba	BA	N244	Northeast	H34	H1 (2)	H20, H21	H5, H6	H1 (2)
61	Itiúba	BA	N257	Northeast	H35	*	H5, H10	H5, H2	H1, H2
61	Itiúba	BA	N258	Northeast	H34	H1 (2)	H22, H23	H5 (2)	H1 (2)
62	Campo Formoso	BA	N581	Southwest	H69	*	H36, H37	H3, H14	H9 (2)
63	Mairi	BA	N242	Northeast	H33	H28, H29	H5, H10	H2 (2)	H1 (2)
64	Itaberaba	BA	N217	Northeast	H26	H1 (2)	H14 (2)	H2 (2)	H2 (2)
65	Lençóis	BA	N761	Northeast	H99	H59 (2)	H14 (2)	H2 (2)	H1, H2
66	Seabra	BA	N223	Southwest	H27	H23 (2)	H15, H16	H3 (2)	H4 (2)
67	Morro do Chapéu	BA	N580	Southwest	H68	H44 (2)	H26, H35	H13 (2)	H8 (2)
67	Morro do Chapéu	BA	N766	Southwest	H100	H60, H61	H36 (2)	H21, H22	H9 (2)
68	Gentio do Ouro	BA	N697	Southwest	H88	H17 (2)	H47, H48	H19 (2)	H5 (2)
68	Gentio do Ouro	BA	N698	Southwest	H89	H17 (2)	H17, H49	H4 (2)	H5 (2)
69	Santo Inácio	BA	N661	Southwest	H80	*	H17 (2)	H4 (2)	H5 (2)
70	Barra	BA	N680	Southwest	H85	*	H44 (2)	H18 (2)	H14 (2)
71	Buritirama	BA	N681	Southwest	H86	H26, H52	H45 (2)	H1 (2)	H6, H14
71	Buritirama	BA	N683	Southwest	H87	H53 (2)	H46 (2)	H1 (2)	H6 (2)
72	Ibotirama	BA	N228	Southwest	H28	H17 (2)	H17 (2)	H4 (2)	H5 (2)
72	Ibotirama	BA	N229	Southwest	H29	H17, H24	H18 (2)	*	H5 (2)
72	Ibotirama	BA	N232	Southwest	H30	*	H19 (2)	H4 (2)	H5 (2)
72	Ibotirama	BA	N233	Southwest	H31	H17, H25	*	H4, H1	H5 (2)
72	Ibotirama	BA	N234	Southwest	H32	H26, H27	H17 (2)	H4 (2)	H5, H6
73	São Desidério	BA	N753	Southwest	H56	H17, H58	H54, H55	H17, H1	H6 (2)
73	São Desidério	BA	N757	Southwest	H98	*	H56, H57	H1 (2)	H6, H15
74	PARNA Cavernas do Peruaçu	MG	N774	Southwest	H101	H62 (2)	H58, H59	H1 (2)	*
75	Montezuma	MG	N744	Southwest	H93	H23 (2)	H53 (2)	H3 (2)	H5 (2)
76	Condeuba	BA	N741	Northeast	H26	H3 (2)	H5, H35	H8, H2	H1 (2)
77	Grão Mogol	MG	N745	Southwest	H96	H56, H57	H17 (2)	H4 (2)	H5 (2)



Map code	Locality	State	Lab code	Population	Haplotypes				
					12S	NKTR	ATPSB	R35	RP40
78	Brasilândia de Minas	MG	N537	Southwest	H63	H41 (2)	H32 (2)	H1 (2)	H6 (2)

\*samples that gene amplification failed; Locality abbreviations: National Park (PARNA), Ecological Station (EE), and National Forest (FLONA); State abbreviations: Alagoas (AL), Bahia (BA), Ceará (CE), Maranhão (MA), Minas Gerais (MG), Paraíba (PB), Pernambuco (PE), Piauí (PI), Rio Grande do Norte (RN), and Sergipe (SE).

Table S7. Tests of nested models in IMa2 for Northeast and Southwest lineages.

Model	#P	log(P)	2LLR	df	P	AIC	ΔAIC
$\Theta_1 \Theta_2 \Theta_A m_1 m_2$	5	1.88	-	-	-	6.232	2.041
$\Theta_2 \Theta_1 = \Theta_A m_1 m_2$	4	-5.92	15.60	1	<0.001	19.834	15.643
$\Theta_1 = \Theta_2 \Theta_A m_1 m_2$	4	1.14	1.49	1	~0.25*	5.724	1.533
$\Theta_1 \Theta_2 = \Theta_A m_1 m_2$	4	-7.84	19.45	1	<0.001	23.680	19.489
$\Theta_1 \Theta_2 \Theta_A m_1 = m_2$	4	1.56	0.66	1	~0.5*	4.888	0.697
$\Theta_1 \Theta_2 \Theta_A m_1 = 0 m_2$	4	-50.80	105.40	1 <sup>†</sup>	<0.001	109.600	105.409
$\Theta_1 \Theta_2 \Theta_A m_1 m_2 = 0$	4	-3.06	9.88	1 <sup>†</sup>	<0.002	14.112	9.921
$\Theta_2 \Theta_1 = \Theta_A m_1 = m_2$	3	-6.97	17.70	2	<0.001	19.932	15.741
$\Theta_2 \Theta_1 = \Theta_A m_1 = 0 m_2$	3	-83.17	170.10	2 <sup>†</sup>	<0.001	172.340	168.149
$\Theta_2 \Theta_1 = \Theta_A m_1 m_2 = 0$	3	-16.99	37.75	2 <sup>†</sup>	<0.001	39.980	35.789
$\Theta_1 = \Theta_2 = \Theta_A m_1 m_2$	3	-8.18	20.13	2	<0.001	22.364	18.173
$\Theta_1 = \Theta_2 \Theta_A m_1 = m_2$	3	0.90	1.96	2	~0.4*	4.191	0
$\Theta_1 = \Theta_2 \Theta_A m_1 = 0 m_2$	3	-50.82	105.40	2 <sup>†</sup>	<0.001	107.640	103.449
$\Theta_1 = \Theta_2 \Theta_A m_1 m_2 = 0$	3	-4.04	11.85	2 <sup>†</sup>	<0.005	14.080	9.889
$\Theta_1 \Theta_2 = \Theta_A m_1 = m_2$	3	-8.32	20.40	2	<0.001	22.636	18.445
$\Theta_1 \Theta_2 = \Theta_A m_1 = 0 m_2$	3	-86.47	176.70	2 <sup>†</sup>	<0.001	178.940	174.749
$\Theta_1 \Theta_2 = \Theta_A m_1 m_2 = 0$	3	-20.53	44.83	2 <sup>†</sup>	<0.001	47.060	42.869
$\Theta_1 \Theta_2 \Theta_A m_1 = 0 m_2 = 0$	3	-100.00	203.80	2 <sup>†</sup>	<0.001	206.000	201.809
$\Theta_2 \Theta_1 = \Theta_A m_1 = 0 m_2 = 0$	2	-122.60	249.00	3 <sup>†</sup>	<0.001	249.200	245.009
$\Theta_1 = \Theta_2 = \Theta_A m_1 = m_2$	2	-8.70	21.18	3	<0.001	21.406	17.215
$\Theta_1 = \Theta_2 = \Theta_A m_1 = 0 m_2$	2	-86.67	177.10	3 <sup>†</sup>	<0.001	177.340	173.149
$\Theta_1 = \Theta_2 = \Theta_A m_1 m_2 = 0$	2	-23.93	51.63	3 <sup>†</sup>	<0.001	51.860	47.669
$\Theta_1 = \Theta_2 \Theta_A m_1 = 0 m_2 = 0$	2	-100.10	204.10	3 <sup>†</sup>	<0.001	204.200	200.009
$\Theta_1 \Theta_2 = \Theta_A m_1 = 0 m_2 = 0$	2	-120.50	244.90	3 <sup>†</sup>	<0.001	245.000	240.809
$\Theta_1 = \Theta_2 = \Theta_A m_1 = 0 m_2 = 0$	1	-122.60	249.00	4 <sup>†</sup>	<0.001	247.200	243.009

Number of demographic parameters (#P); log of the posterior probability (log(P)); log-likelihood ratio statistics (2LLR); degrees of freedom (df); <sup>†</sup>test distribution of 2LLR is a mixture; \*the model was not rejected by the 2LLR test in favor of the full model  $\Theta_1 \Theta_2 \Theta_A m_1 m_2$  with  $p < 0.05$ .

Table S8. Population parameter estimates in IMA2 for Northeast and Southwest lineages.

<b>Value</b>	<b>N<sub>1</sub></b>	<b>N<sub>2</sub></b>	<b>N<sub>A</sub></b>	<b>m<sub>1</sub></b>	<b>m<sub>2</sub></b>	<b>2N<sub>1</sub>m<sub>1</sub></b>	<b>2N<sub>2</sub>m<sub>2</sub></b>	<b>t</b>
HiPt	5,106,416	6,311,366	497,188	0.0812	0.0421	0.4075	0.2625	9,751,909
Mean	5,186,902	6,507,033	813,707	0.0935	0.0606	0.4607	0.3734	10,551,274
Lo 95% HPD	4,053,547	4,708,665	29,246	0.0344	0.0043	0.1763	0.0288	6,794,516
Hi 95% HPD	6,358,160	8,428,803	1,830,823	0.16	0.1285	0.7757	0.7908	14,768,246

The units on population size estimates for N<sub>1</sub> (Northeast), N<sub>2</sub> (Southwest) and the ancestral population (N<sub>A</sub>) are individuals; m<sub>1</sub> is the mutation scaled migration rate per generation per gene at which Northeast receives genes from Southwest and m<sub>2</sub> is the reverse; 2N<sub>1</sub>m<sub>1</sub> is the population migration rate at which the genes of Northeast are supplanted by genes from Southwest and 2N<sub>2</sub>m<sub>2</sub> is the reverse; time since splitting (t) is in number of years.

Fig. S1. Haplotype network for 12S (A), RP40 (B), NKTR (C), R35 (D) and ATPSB (E) using median-joining method. Each haplotype is represented by a circle whose area is proportional to its frequency. White and gray circles represent Northeast and Southwest lineages, respectively. Numbers represent mutational differences. Median vectors (unsampled or extinct haplotypes) is not shown.

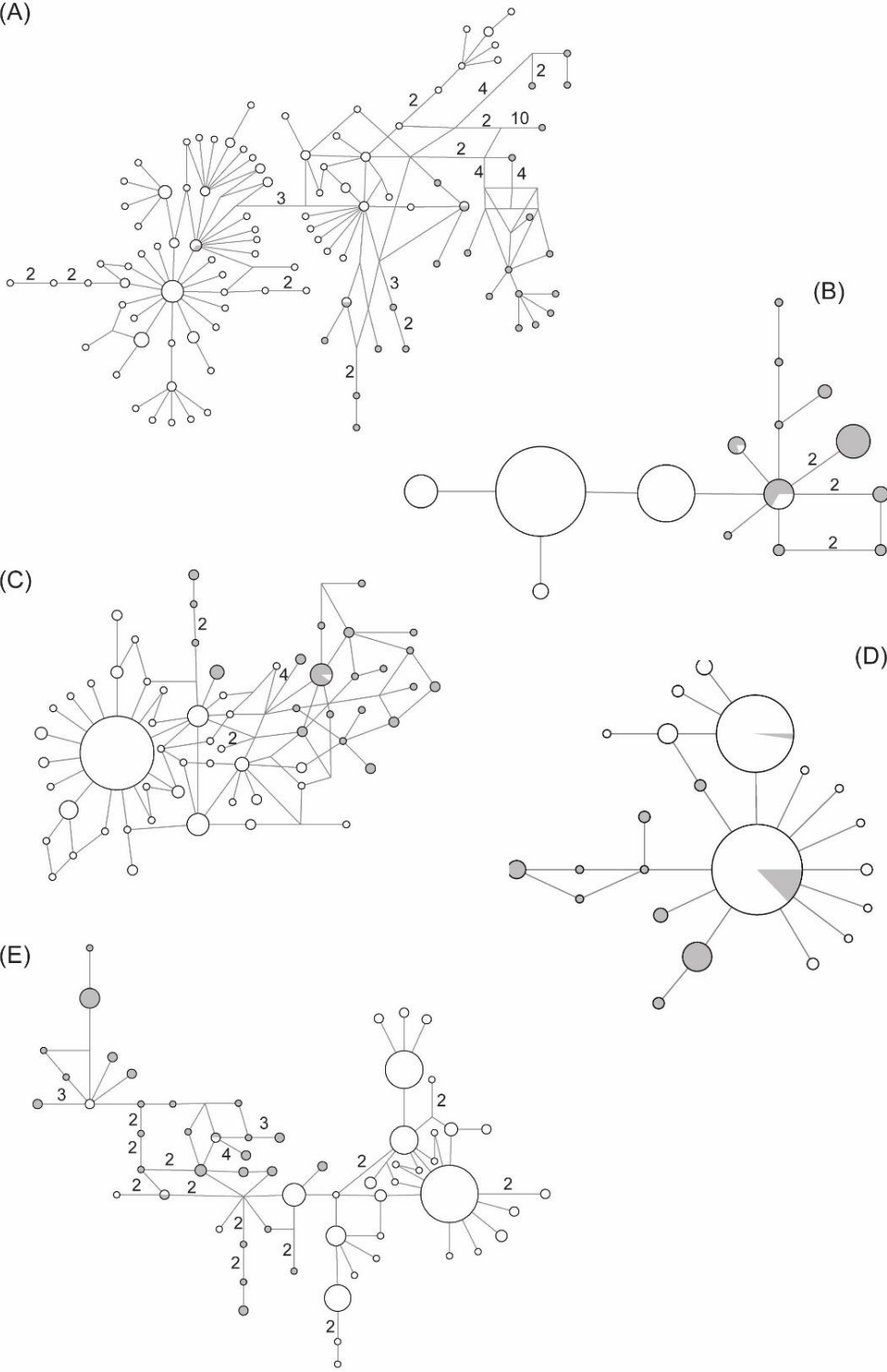


Fig. S2. STRUCTURE results showing (A) plot of the log-likelihood value ( $\text{LnPr}(X|K)$ ) versus the number of potential populations ( $K$ ), (B) plot of Evanno  $\Delta K$  method to evaluate the most supported  $K$  based on rate of change of the likelihood distribution as a function of  $K$ , and (C) plot of ancestry estimates, which represent the estimated membership for  $K$ -inferred clusters.

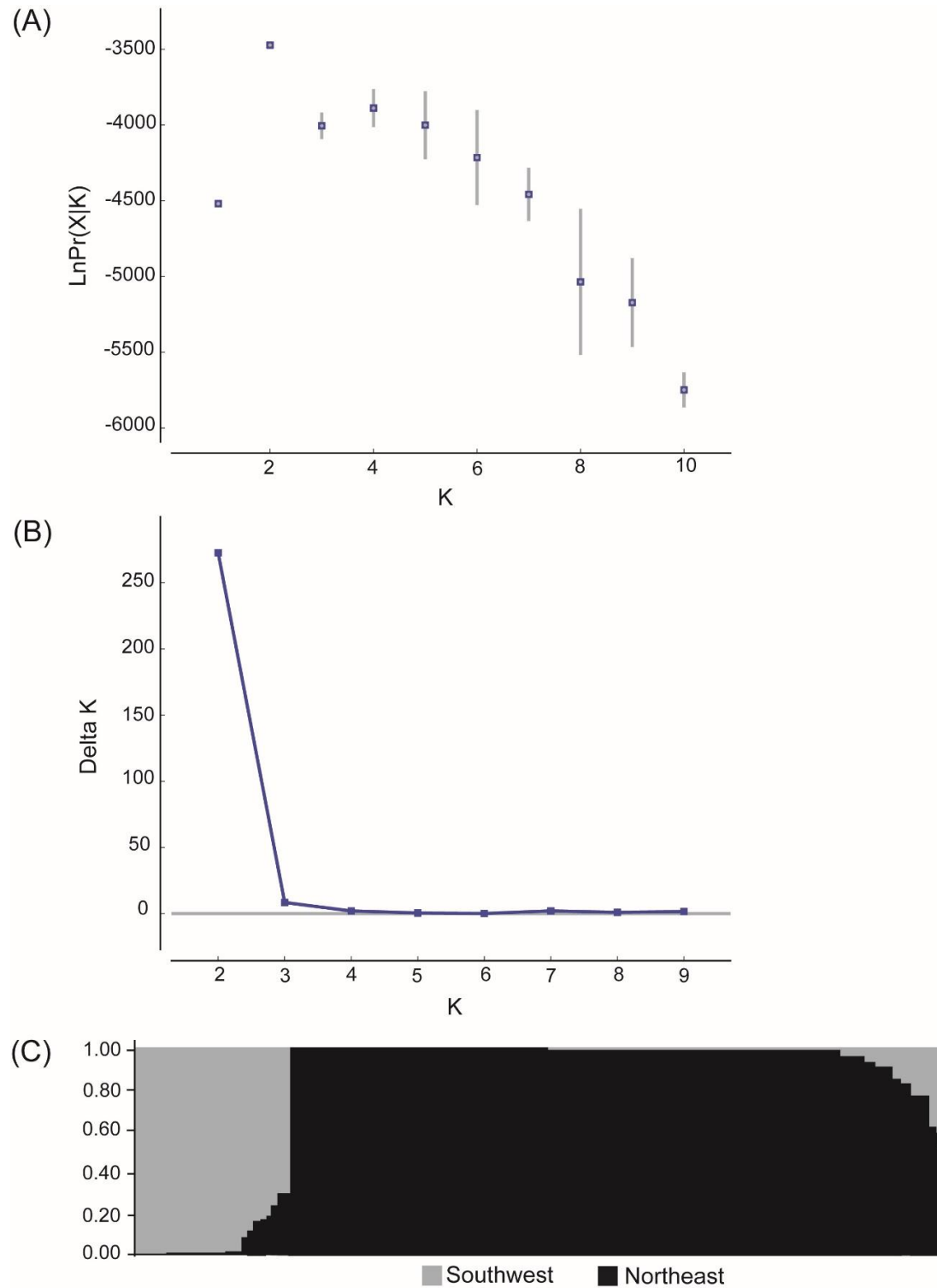


Fig. S3. Gene trees for 12S (A), RP40 (B), ATPSB (C), R35 (D) and NKTR (E) inferred using Bayesian inference in the program BEAST. Gray branches represent the Southwest lineage and the other branches indicate the Northeast lineage. Posterior probabilities of 100% and  $\geq 95\%$  are indicated by asterisk and filled circles, respectively. Terminal names of samples (137 in total) are available in Table S6 (Supporting information), together with additional information.

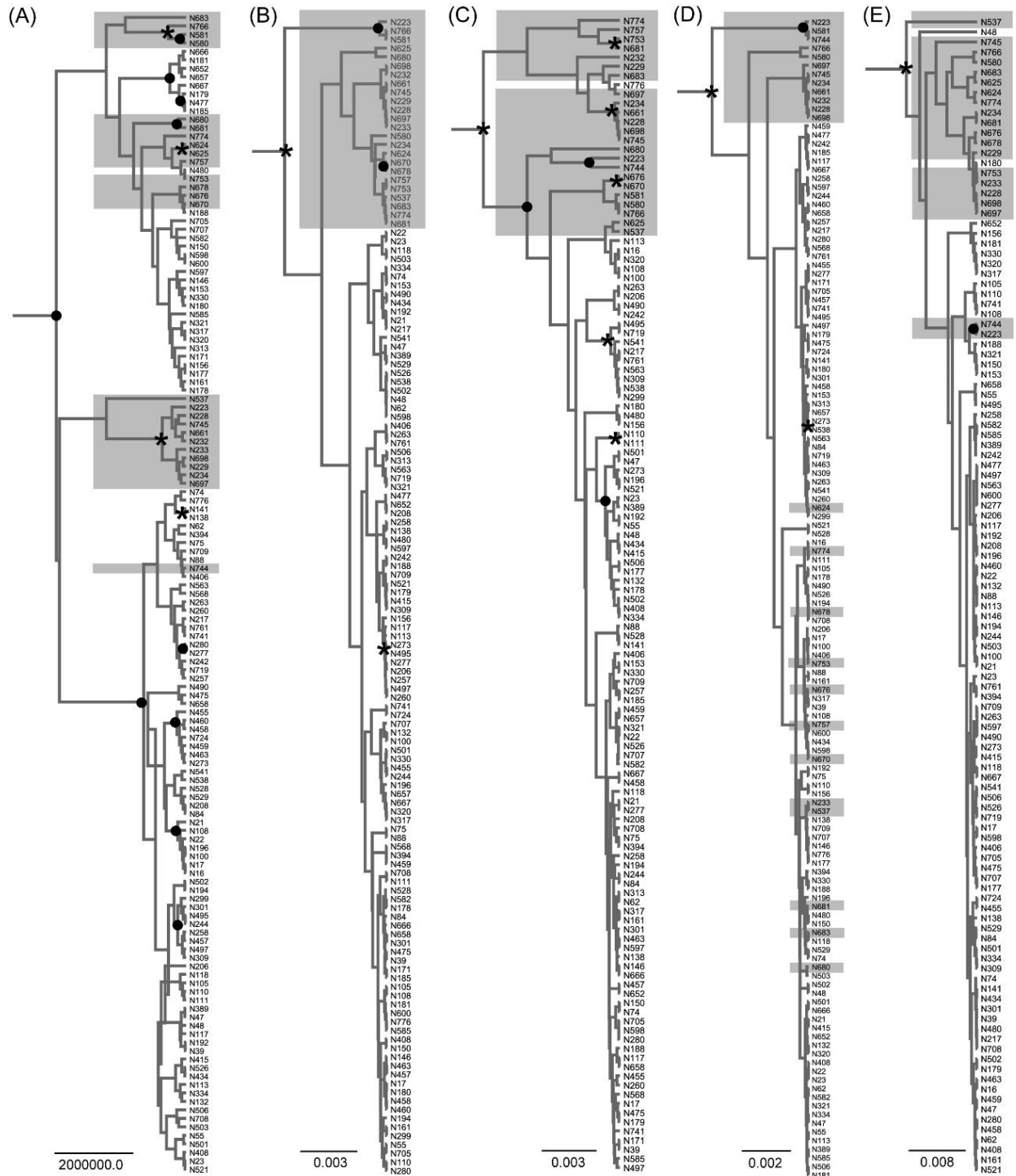
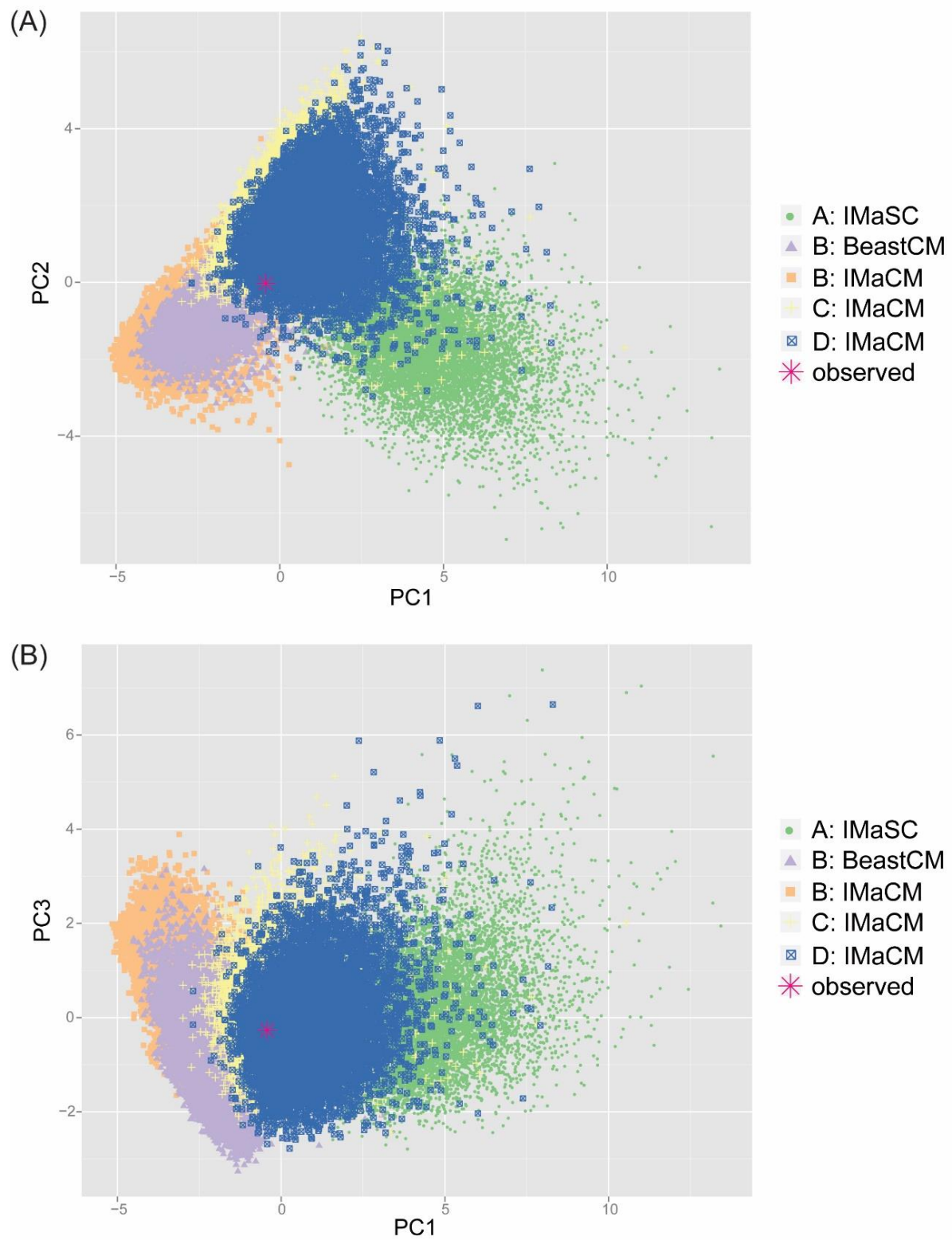


Fig. S4. Principal Components Analysis vectors predictive plots, PC1  $\times$  PC2 (A) and PC1  $\times$  PC3 (B), for the prior predictive distributions of summary statistics for the five best models (see Table 4) compared using the Approximate Bayesian Computation approach.



## CAPÍTULO II

Influence of landscape features on genetic diversity and differentiation in Brazilian whiptail  
lizard (*Cnemidophorus ocellifer*)



Influence of landscape features on genetic diversity and differentiation in Brazilian whiptail lizard (*Cnemidophorus ocellifer*)

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## **Abstract**

Spatial patterns of genetic variation can help understand how specific environmental factors either permit or restrict gene flow and create opportunities for regional adaptations. Organisms typical of harsh environments, such as the Brazilian Caatinga biome, are especially interesting as they can reveal how severe climate conditions affect genetic diversity. Here, we combine information from mitochondrial DNA, physical and climatic environmental features to study the association between different aspects of the Caatinga landscape and spatial genetic variation in the whiptail lizard *Cnemidophorus ocellifer*. We investigated which of the climatic, geographical and/or historical components best predict: (1) the spatial distribution of genetic diversity, and (2) the genetic differentiation among populations. We found that genetic variation in *C. ocellifer* has been influenced mainly by temperature variability that seems to modulate connectivity among populations. Past climate conditions were important in shaping the currently observed genetic diversity, suggesting a time lag in genetic responses. Population structure in *C. ocellifer* was best explained by both isolation by distance and isolation by resistance (differences in niche suitability and main rivers). Our findings indicate that both physical and climatic features are important to explain the observed patterns of genetic variation in whiptail lizard *C. ocellifer*.

*Keywords:* Caatinga, ecological niche modelling, dispersal, gene flow, population genetic

## Introduction

Genetic diversity and structure are usually not evenly distributed across the landscape and many factors may influence this spatial heterogeneity (e.g. Funk *et al.* 2005; Pérez-Espona *et al.* 2008; Pease *et al.* 2009; Ortego *et al.* 2012; Lawson 2013). Processes that reduce or increase dispersal rate efficiency between populations may influence the spatial patterns of genetic variation (Storfer *et al.* 2006; Anderson *et al.* 2010; Sork & Waits 2010; Zeller *et al.* 2012). In this case, landscape and environmental features may reduce or enhance connectivity among populations. In addition, given habitat preferences and ecological niche, dispersal matrices may show different levels of permeability (e.g. Funk *et al.* 2005; Pérez-Espona *et al.* 2008; Pease *et al.* 2009; Ortego *et al.* 2012; Lawson 2013). Recent human-induced shifts in landscape such as habitat fragmentation and large roads may also impact gene flow (e.g. Pérez-Espona *et al.* 2008; Zellmer & Knowles 2009). Thus, understanding how landscape and environmental features can shape genetic variation is an important step to understand population dynamics, species distribution range, evolutionary trajectories and speciation, and may ultimately help improve species management and conservation (Storfer *et al.* 2006; Sork & Waits 2010; Zeller *et al.* 2012).

Isolation by distance (hereafter IBD) is the correlation of linear geographic distances and genetic distances among populations, and it is one of the most well documented patterns of genetic differentiation. IBD occurs when gene flow is reduced among populations located at greater distances from each other (Wright 1943; Jenkins *et al.* 2010). Although IBD is very commonly detected among a wide range species (see review in Jenkins *et al.* 2010), incorporating landscape complexity may help to generate more realistic models to understand gene flow among populations, spatial patterns of genetic variation, and local adaptation (Storfer *et al.* 2006; Anderson *et al.* 2010; Sork & Waits 2010; Zeller *et al.* 2012).

Physical aspects of the landscape have potential to act as barriers, affecting spatial connectivity and rates of gene flow among populations. Rivers and mountains have been frequently implicated in abrupt genetic breaks (e.g. Funk *et al.* 2005; Lawson 2013), and may ultimately facilitate allopatric speciation (Soltis *et al.* 2006). However, some physical aspects vary more tenuously in the landscape and yet may strongly affect the patterns of dispersal and gene flow. For example, elevation and slope gradients have been associated with increased genetic differentiation among populations (e.g. Funk *et al.* 2005; Wang 2009), even in species with high potential for gene flow (Pérez-Espona *et al.* 2008; Ortego *et al.* 2012). In this case, energetic costs of moving up steep slopes, natural selection against nonlocal genotypes, and/or asynchrony in reproductive phenology may have generated patterns of reduced gene flow along these gradients (Funk *et al.* 2005; Pérez-Espona *et al.* 2008; Ortego *et al.* 2012).

Present and past environmental conditions may also influence current distribution of genetic variability (Anderson *et al.* 2010). For instance, historically stable areas (i.e. refugia) can favor progressive genetic diversification and sustain more genetically diverse populations than unstable areas (Carnaval *et al.* 2009). In addition, populations experiencing contrasting environmental conditions have shown genetic differentiation, even in highly mobile species (e.g. Pease *et al.* 2009), and relatively small distribution ranges (e.g. Ortego *et al.* 2012). Thus, understanding how suitable niches are spatially and temporally distributed can be useful to identify corridors for gene flow as well as for detecting populations in areas with low habitat suitability or isolated by patches of unsuitable niche (Pease *et al.* 2009; Ortego *et al.* 2012; Lawson 2013).

Phylogeographic history of an organism can also shape its contemporary genetic patterns (Sork & Waits 2010). For instance, when the impact of environmental heterogeneity on the colonization process is taken into account the range expansion itself becomes a likely candidate for generating significant genetic differentiation (Knowles & Alvarado-Serrano

2010). Hence, the spatial and temporal history of colonization process can allow us to create a more accurate picture of how genetic variation is distributed across a species' range. Thus, historical events must be considered for a comprehensive understanding of the observed patterns of genetic variation (Sork & Waits 2010).

Examining genetic variation in organisms inhabiting harsh environments such as desert or arid regions can reveal specific requirements for population persistence under difficult conditions (Wang 2009). The Caatinga biome in northeastern Brazil represents the largest, most isolated and species-rich nucleus of Seasonally Dry Tropical Forests, and it is characterized by semiarid vegetation, high temperatures and severe dry seasons (Werneck 2011; Werneck *et al.* 2011). Intuitively, the availability of water per se appears to be a limiting factor for survival under very hot and arid conditions (Hawkins *et al.* 2003). Indeed, Caatinga species diversity has been influenced by water-energy balance, and variance in temperature and precipitation (De Oliveira & Diniz-Filho 2010). Hence, the Caatinga biota offers an excellent opportunity to study the contribution of severe climatic conditions in defining patterns of genetic variation.

Here we evaluated the relative importance of different mechanisms such as IBD, physical barriers, environmental conditions, current and past climate, and colonization events in shaping the spatial genetic variation in the whiptail lizard *Cnemidophorus ocellifer* (Spix 1825). The *Cnemidophorus ocellifer* species complex from Caatinga was recently investigated using coalescent methods and model-based approach through multilocus markers and *C. ocellifer* was recognized as the most common whiptail lizard in this biome (Oliveira *et al.* In prep). Phylogeographic reconstructions suggested that ancestral population of *C. ocellifer* originated in central-north Caatinga and subsequently expanded north, east and south Caatinga, colonizing the entire biome (see Oliveira *et al.* In prep). Therefore, *C. ocellifer* is a

well-suited organism for this study due to its widespread distribution range in Caatinga biome and its known phylogeographic history.

We combined information from genetic data, ecological niche modelling, and phylogeographic history of *C. ocellifer* to test the correlation of landscape and environmental features to genetic diversity and differentiation among populations. We investigated the role of niche suitability and stability, water and energy availability, environmental heterogeneity, and colonization events in the spatial distribution of *C. ocellifer* genetic variability. We also investigated whether geographical distance, connectivity in terms of suitable habitat between populations, the effect of slope and rivers may explain genetic breaks. Our findings highlight how habitat, climate and geography interact to impact the accumulation of genetic diversity and its differentiation throughout the Caatinga xeric biome.

## **Materials and Methods**

### ***Sample collection and sequencing***

From fieldwork and collection loans, we obtained 336 tissue samples from 46 localities distributed along *C. ocellifer* distribution range (Fig. 1 and Table S1, Supporting information). Average sample size per localities was seven individuals, with a minimum of four and a maximum of 16 individuals (Table 1). We extracted DNA from liver or muscle tissue, and sequenced all 336 individuals for 12S mitochondrial gene (12S). Extraction, amplification and sequencing are described in Oliveira *et al.* (In prep), as well as the primers used here. Following a similar procedure described by Oliveira *et al.* (In prep), we removed gaps of 12S gene using Gblocks program (Talavera & Castresana 2007). All sequences obtained in this study are available at GenBank (access numbers available after acceptance for publication).

### ***Genetic diversity and differentiation***

To access genetic diversity we calculated haplotype number ( $h$ ), haplotype diversity ( $Hd$ ), and nucleotide diversity ( $\pi$ ) for each locality using DnaSP 5.10 program (Librado & Rozas 2009). Each locality was considered as a population. Although localities have different number of samples, the genetic diversity (i.e.  $\pi$ ) is independent of sample size ( $r = 0.026$ ;  $P = 0.862$ ). To access genetic differentiation we calculated genetic distance among 46 sampling locations through pairwise  $F_{ST}$ -values and tested their significance using 10,000 permutations in ARLEQUIN 3.5 (Excoffier & Lischer 2010). This analysis resulted in a matrix of pairwise  $F_{ST}$ -values (Table S2, Supporting information). We also estimated the genealogical relationships among haplotypes to visualize the genetic diversity and structure in *C. ocellifer*. First, we implemented Maximum Likelihood (ML) approach in software PHYML 3.1 (Guindon *et al.* 2010), using default options and the best-fit model for 12S (i.e. HKY) inferred using Bayesian Information Criterion (BIC) in the program jModeltest (Posada 2008). We then used the ML tree to estimate the network haplotype in Haploviewer program (Salzburger *et al.* 2011).

To illustrate the spatial distribution of genetic variation in *C. ocellifer*, we generated maps by interpolating both genetic diversity and differentiation across our study region. Interpolation provides a way to predict values and corresponding levels of uncertainty for the variable of interest between points where observations have been made. We used  $\pi$  values from sampling localities and average pairwise genetic distance ( $F_{ST}$ ) of each locality to generate interpolated genetic variation maps. Using the R package ‘geoR’ (Ribeiro Jr & Diggle 2001), we derived the final raster maps through the interpolation of ML values by Gaussian process regression (kriging) for non-sampled localities.

### ***Ecological niche modelling***

We used ecological niche modelling (ENM) to estimate the geographic distribution of climatically suitable regions for *C. ocellifer*. ENM results were used to analyze whether current or past climatic conditions are responsible for patterns of genetic diversity and differentiation in *C. ocellifer* (see below). We used all 46 localities from the present study plus additional 45 confirmed records from Oliveira *et al.* (In prep) as species occurrence dataset (Table S3, Supporting information). We first modelled *C. ocellifer* climatically suitable regions for current climatic conditions and then projected it into three past climatic scenarios: mid-Holocene (6 thousands years before the present; 6 kyr), Last Glacial Maximum (LGM, 21 kyr) and Last Interglacial (LIG, ~130 kyr). Present climatic variables were downloaded from the WorldClim database (see <http://www.worldclim.org/> for variable descriptions) interpolated to 2.5 arc-min resolution (Hijmans *et al.* 2005). We obtained past climate data for the mid-Holocene and LGM from ECHAM3 atmospheric General Circulation Model (GCM; DKRZ, 1992) available at the Palaeoclimatic Modelling Intercomparison Project webpage (PMIP; <http://pmip.lsce.ipsl.fr/>), and for the LIG from Otto-Bliesner *et al.* (2006).

To avoid over-prediction and low specificity, we cropped the bioclimatic layers to span from latitude 0 to -20 and longitude -50 to -34 (values in decimals degrees). This background encompassed the current extent of Caatinga and adjacent areas. To avoid model overparameterization, we removed strongly correlated variables ( $r > 0.85$ ) based on their biological relevance for *C. ocellifer*. We built our models using 11 out of 19 original environmental variables (see Results). We used values of permutation importance (i.e. the loss of model predictive power when each variable is excluded) to determine variables importance.

We implemented ENM in R platform vs. 3.1 (R Core Team, 2015) using the maximum entropy algorithm (Phillips & Dudik 2008) and ‘dismo’ package (Hijmans *et al.* 2013). First,



we trained the model under current climatic scenarios based on 75% of randomly selected presence records and used the remaining 25% to test the model in 20 bootstrap repetitions. We evaluated the model performance using the area under the curve (AUC) for the test data. AUC statistics assess the sensitivity (absence of omission error) and the specificity (absence of commission error) of a model (Fielding & Bell 1997). AUC value of 0.50 indicates model performance compared to null expectations (random prediction), while higher AUC values indicate better models, with maximum prediction being 1 (Hanley & Mcneil 1982).

### *Effect of historic and environmental factors on genetic diversity*

We used  $\pi$  values to represent the genetic diversity. We tested five plausible hypotheses that may explain genetic diversity in *C. ocellifer*: (i) Niche suitability, (ii) Niche stability, (iii) Water and energy availability, (iv) Environmental heterogeneity, and (v) Colonization. These hypotheses are not mutually exclusive and two or more hypotheses combined may better explain the genetic pattern. Explanatory variables related to each hypothesis are described below in each subtopic (see also Table 2). Using R ‘raster’ package (Hijmans & van Etten 2014) and several databases (described below), we extracted environmental data for all 46 localities with genetic information. All environmental values are available at Table S4, Supporting information.

#### *Niche suitability hypothesis*

Considering that niche suitability increases the probability of a population to persist in the environment, we expect that the genetic variability should be higher in areas with high habitat suitability and lower in areas with low habitat suitability. Past environmental conditions may also have an important influence on the current genetic variability (Anderson *et al.* 2010). Thus, we also predict that genetic diversity should be higher in areas with high suitability

during the past. Because LGM experienced the most extreme climatic conditions, we used only LGM values to represent past climate. We implemented two alternative approaches to test this hypothesis and they assume the same assumptions cited above. First, we directly assessed the current and LGM niche suitability of *C. ocellifer* by extracting values from ENM results. As a second approach, we used only the three most important variables in the ENM (isothermality - Bio3; temperature seasonality - Bio4; and minimum temperature of coldest month - Bio6) as a simplified measure of *C. ocellifer* niche suitability since they together explain 73% of the model (see Results). A possible advantage is that this approach does not consider less important variables that could be masking the influence of the three main variables. In addition, these three variables were positively and significantly associated to ENM (Table S5, Supporting information). Bio3 represents the quantification of how large the daily temperature oscillation is in comparison to the annual oscillation, whereas Bio4 is annual range in temperature. From WorldClim and ECHAM3 atmospheric GCM database, we extracted current and LGM values of the Bio3, Bio4 and Bio6 variables.

#### *Niche stability hypothesis*

Regions that have experienced higher climatic variation over time are likely to have suffered more dramatic changes in habitat structure and are considered to be more instable when compared to regions that have experienced little change through time. Stable regions are likely to have had higher population persistence and sheltered higher population sizes through climatic fluctuations when compared to instable areas (Carnaval *et al.* 2009). Therefore, we expect that genetic diversity should be positively associated with stability. To obtain a stability map that represent regions where the suitable climate for *C. ocellifer* has persisted since the LIG, we overlapped the presence/absence projections of each climatic scenario (current, mid-Holocene, LGM, and LIG) generated in ENM. We then obtained a map with

values ranging from 0 (unsuitable climate in all climate projections) to 4 (suitable climate in all climate projections).

#### *Water and energy availability hypothesis*

Four variables represented this hypothesis: annual mean temperature (Bio1) and annual precipitation (Bio12) were used as a direct measure of energy and water availability, respectively; actual evapotranspiration (AET) and net primary productivity (NPP) were used as measure of the water-energy balance. Temperature and/or water availability can accelerate evolutionary rates (Allen *et al.* 2002) and maintain high genetic diversity by increasing the rate of biotic interactions (Moya-Laraño 2010). We then predict that genetic variability should increase with water and energy availability. We extracted values for Bio1 and Bio12 from WorldClim database. AET and NPP values were extracted from the FAO GeoNetwork (<http://www.fao.org/geonetwork/srv/en/main.home>) and National Aeronautics and Space Administration (NASA; <http://daac.ornl.gov/>) webpages, respectively.

#### *Environmental heterogeneity hypothesis*

We used data on the topographic complexity as a surrogate for environmental heterogeneity. We expect that genetic diversity should be higher in areas with high environmental heterogeneity due to local adaptations that lead to small-scale genetic differentiation (Garant *et al.* 2005). In order to generate a topographic complexity index, we used altitude data at a 30'' spatial resolution (1km) from NASA webpage ([www2.jpl.nasa.gov/srtm/](http://www2.jpl.nasa.gov/srtm/)). Next, we aggregated the 10 nearest cells and used the standard deviation of their altitudes as the estimated value of topographic complexity for the new cells of lower resolution.

#### *Colonization hypothesis*

This hypothesis take into account the distance of each locality to *C. ocellifer* center of origin. Areas closer to the center of origin presumably had more time to accumulate genetic diversity due to an earlier colonization. We predict that genetic diversity should be negatively related to geographic distance from *C. ocellifer* center of origin. Using phylogeographic reconstruction, Oliveira *et al.* (In prep) defined the *C. ocellifer* center of origin through multilocus markers. We overlapped origin polygons of all genes (12S, ATPSB, NKTR, R35, and RP40) used by Oliveira *et al.* (In prep) and calculated its centroid. The geographic coordinates of this centroid were used as an estimate of the center of origin. Using R package ‘ecodist’ (Goslee & Urban 2007), we calculated the Euclidean geographical distances between each locality and *C. ocellifer* center of origin.

#### *Statistical analyses: genetic diversity*

In order to analyze genetic diversity patterns under the hypotheses proposed above, we initially performed a linear regression analysis between  $\pi$  (response variable) and explanatory variables related to each hypothesis (see Table 2). We then assessed model performance and used the variance inflation factor (VIF) as a measure of the degree of collinearity present in the data (see Dormann *et al.* 2013). Collinearity is common in ecological data and can be a problem inflating the estimate of regression parameters, leading to wrong identification of relevant predictors in a statistical model (Dormann *et al.* 2013). By comparing the predictor variables, we removed one by one those with higher VIF values (Dormann *et al.* 2013). In the end, all variables retained in each statistical model presented  $VIF < 3$ . We had to take into account the probable spatial structure (autocorrelation) underlying these ecological data, which could inflate the Type I error of the significance levels due to non-independence of the data. Using Moran’s *I* coefficient, we measured this non-independence in model residuals. Moran’s *I* coefficient were calculated for 10 geographic distance classes, generating a spatial

correlogram, which usually ranges between 1 (positive autocorrelation) to -1 (negative autocorrelation) (Legendre 1993). Because autocorrelation was observed in some model residuals (see Results; Figs S1 and S2, Supporting information), we also performed univariate and multivariate simultaneous autoregression (SAR). We used Akaike's Information Criterion (AIC) to select the best model fitting the data. We then compared models by calculating the difference between AIC of each model and the minimum AIC found for the set of models compared ( $\Delta AIC$ ; Burnham & Anderson 2002; Diniz-Filho *et al.* 2008). Lower  $\Delta AIC$  scores indicate closer fit to the best model and models with differences among  $\Delta AIC > 2$  were considered statistically different (Burnham & Anderson 2002). We built SAR models and performed model selection using the software SAM 4.0 - Spatial Analysis in Macroecology (Rangel *et al.* 2010).

### ***Effect of isolation by distance versus isolation by resistance on genetic differentiation***

We considered *a priori* six potential drivers of genetic differentiation in *C. ocellifer*: (i) Geographical distance, (ii) Connectivity through differences in the current niche suitability ( $NS_{CURRENT}$ ), (iii) Connectivity through differences in the LGM niche suitability ( $NS_{LGM}$ ), (iv) Resistance through differences in terrain slope, (v) Resistance through differences in terrain roughness, and (vi) Resistance of rivers. The first hypothesis (geographical distance) represents the probable pattern of IBD of the genetic differentiation, whereas other hypotheses are based on assumptions regarding the permeability of landscape features to dispersal and represent the probable isolation by resistance pattern. These hypotheses are not mutually exclusive and two or more hypotheses combined may better explain the genetic pattern. Explanatory variables related to each hypothesis are described below in each subtopic (see also Table 2).

### *Isolation by distance hypothesis*

We calculated a matrix of pairwise Euclidean geographical distances among all 46 localities (Table S6, Supporting information) using R ‘ecodist’ package (Goslee & Urban 2007).

Considering that *C. ocellifer* has a large distribution area, we expect that genetic differentiation increases with geographical distance simply due to the restricted gene flow between populations located far from each other, corroborating IBD pattern.

### *Isolation by resistance hypotheses*

We used circuit theory to calculate the environmental cost of all possible routes connecting pairs of populations and identify the corridor with the least environmental resistance using the program CIRCUITSCAPE 3.5.8 (McRae & Beier 2007). We applied this method for slope, roughness, and rivers, as well as  $NS_{CURRENT}$  and  $NS_{LGM}$  rasters obtained from ENM analyses. Following methods described by Wilson *et al.* (2007), we derived roughness from altitude using R package ‘raster’ (Hijmans & van Etten 2014). We calculated roughness for each grid cell as the difference between the maximum and minimum altitude value of the eight surrounding grids cells. Roughness is an indication of how the surface complexity changes over the study area. We used weighting coefficients for the nearer elevation values (eight grid cells) to derive a slope surface (Horn 1981). These weightings are proportional to the reciprocal of the square of the distance from the central grid cell. Through the slope is possible to identify flat areas that tend to facilitate dispersal. Our river raster comprises the main perennial rivers in the Caatinga. Because CIRCUITSCAPE interprets values of 0 as hard barriers, we changed all values of 0 to 0.0001, following a similar procedure described by Lawson (2013). In total we used CIRCUITSCAPE to generate three matrices of connectivity distances ( $NS_{CURRENT}$ ,  $NS_{LGM}$  and rivers) and two matrices of resistance distances (slope and roughness). All matrices are available in the Supporting information (Tables S7-S11). We

predict that landscape features can constrain genetic connectivity among populations due to the restricted gene flow imposed by some barriers. In this case, genetic differentiation should be better explained by pattern of isolation by resistance than merely for pattern of isolation by distance.

#### *Statistical analyses: genetic differentiation*

We conducted analyses of multiple regression on distance matrices (MRM) with 1000 permutations using the R package ‘ecodist’ (Goslee & Urban 2007). Because our original data is best expressed in the form of pairwise distance matrices and the hypotheses to be tested are strictly formulated in terms of distances, Mantel test and its derived forms (e.g. MRM) are one of the few appropriate tests in such situations (Legendre & Fortin 2010). First, we performed simple correlation between the pairwise  $F_{ST}$ -values matrix (response variable) and each explanatory matrix. To measure the degree of collinearity among explanatory variables (see Dormann *et al.* 2013), we assessed the VIF of all variables significantly correlated to  $F_{ST}$ , retaining only those with  $VIF < 3$ . We then performed multiple correlation and the best models were selected according to their AIC scores. We adjusted AIC values to  $\Delta AIC$  values to facilitate the comparison among models. Lower  $\Delta AIC$  scores indicate closer fit to the best model and models with  $\Delta AIC > 2$  were considered statically different (Burnham & Anderson 2002).

## **Results**

### *Genetic diversity and differentiation*

The 336 sequences of 12S gene preserved ~ 95% (375 bp) of its original size and corresponded to 88 distinct haplotypes (Fig. 1). The maximum number of haplotype per locality was eight and the minimum was one (Table 1). The haplotype H2 was the most

widespread, occurring in 17 different localities in north-northeastern Caatinga. Nucleotide diversity per locality ranges from 0 to 0.01067 (Table 1). Genetic diversity in *C. ocellifer* is not uniformly distributed across the species range (Fig. 2A). The highest genetic diversity is concentrated in two patches in central-eastern Caatinga.

Pairwise  $F_{ST}$  values ranged from 0 to 1, and 919 of the 1035 pairwise comparisons were significant (Table S2, Supporting information). Localities with highest mean genetic distance in *C. ocellifer* are concentrated in two patches in central-southern Caatinga and along the eastern coastline (Fig. 2B). The very small genetic distances in northeastern Caatinga (indicated by the largest blue area on Fig. 2B) correspond to the distribution of the most widespread haplotype H2.

#### *Ecological niche modelling*

The climatic variables included in the final habitat suitability model and their values of percent contribution and permutation importance are shown in Table 3. The three most important variables for the model, measured as the percent drop in test AUC when the variable is excluded (permutation importance), were temperature seasonality (Bio4, 39.7%), isothermality (Bio3, 18.5%), and minimum temperature of coldest month (Bio6, 14.9%). The average training AUC for the replicate runs was 0.925 (SD = 0.010; n = 20 replicate model runs), indicating a high performance model (Fielding & Bell 1997).

The distribution of climatically suitable regions for *C. ocellifer* suggests a decrease in habitat suitability over the species distribution range from current to LIG period (Fig. 3). The current and mid-Holocene predictions did not differ substantially and suggest innumerable suitable habitats in the Caatinga domain and adjacent coastline areas, whereas the largest patches of unsuitable habitats are concentrated in the extreme southwest and northwest of Caatinga. LGM predictions showed a range contraction of suitable areas for *C. ocellifer*,



which are restricted in a narrow corridor that extends from center to northeast of the Caatinga region. LIG models suggest low suitability areas for *C. ocellifer* in most part of Caatinga domain. In this period, favorable climates distribute in the central-western of the Caatinga and outside of its current geographic boundaries.

#### *Effect of historic and environmental factors on genetic diversity*

Among five hypotheses tested to explain genetic diversity (Table 4), two were significant: niche suitability, and water and energy availability. Genetic diversity was positively associated with niche suitability in both LGM (Bio3<sub>LGM</sub> + Bio4<sub>LGM</sub>; AIC = -427.465,  $\Delta$ AIC = 0,  $P < 0.001$ ) and current climates (Bio3<sub>CURRENT</sub> + Bio4<sub>CURRENT</sub>; AIC = -427.161,  $\Delta$ AIC = 3.3,  $P < 0.001$ ). In addition, genetic diversity was negatively associated with annual precipitation (Bio12; AIC = -414.834,  $\Delta$ AIC = 12.6,  $P = 0.036$ ). Because the five hypotheses are not mutually exclusive, we tested all combinations of explanatory variables. The model that mixed variables from both current and LGM niche suitability (Bio3<sub>LGM</sub> + Bio4<sub>CURRENT</sub>) explained genetic diversity (AIC = -429.369,  $\Delta$ AIC = 0.1,  $P < 0.001$ ) as well as the LGM niche suitability model (Bio3<sub>LGM</sub> + Bio4<sub>LGM</sub>; AIC = -427.465,  $\Delta$ AIC = 0,  $P < 0.001$ ). Altogether, these two models show that factors related to temperature variability play an important role in driving genetic diversity patterns in *C. ocellifer*. Areas with higher temperature variability (i.e. more suitable niche) generally have higher genetic diversity (Table S12, Supporting information). Past climate conditions were important for shaping genetic diversity since both models included LGM conditions. Our results supports the hypothesis of niche suitability as the best explanation for genetic diversity in *C. ocellifer*.

#### *Effect of isolation by distance versus isolation by resistance on genetic differentiation*

Among six hypotheses tested to explain genetic differentiation in *C. ocellifer*, three were significantly correlated to  $F_{ST}$  (Table 5): connectivity through differences in the  $NS_{CURRENT}$  ( $P = 0.0070$ ,  $AIC = 130.596$ ,  $\Delta AIC = 66.3$ ), resistance of rivers ( $P = 0.0012$ ,  $AIC = 90.203$ ,  $\Delta AIC = 26$ ), and geographical distance ( $P < 0.001$ ,  $AIC = 90.096$ ,  $\Delta AIC = 25.8$ ). We found low degree of collinearity ( $VIF < 3$ ) among these three hypotheses. Because they are not mutually exclusive, the best models were a combination of multiple hypotheses. Two multiple models explained genetic differentiation in *C. ocellifer* and were considered statistically equivalent: rivers + geographic distance ( $AIC = 64.253$ ,  $\Delta AIC = 0$ ,  $P = 0.0017$ ) and  $NS_{CURRENT}$  + rivers + geographic distance ( $AIC = 66.114$ ,  $\Delta AIC = 1.9$ ,  $P < 0.001$ ). Our results suggest that gene flow in *C. ocellifer* is influenced by combination of isolation by distance and isolation by resistance patterns (rivers and suitable climate).

## **Discussion**

Finer-scale process may have played an important role in intraspecific diversification of Caatinga endemic species. However, it is unknown how habitat, climate and geography interact to shape the accumulation of genetic diversity and its differentiation throughout this xeric biome. In this article, we used a densely sampled case study of common and broadly distributed species of lizard. Our findings indicate that both climatic and physical features interact to explain observed patterns of genetic variation in the whiptail lizard *C. ocellifer*.

### *Effect of historic and ecological factors on genetic diversity*

Climatic fluctuations can alter the spatial and temporal availability of suitable niche modifying distribution ranges (see Pease *et al.* 2009; Ortego *et al.* 2012; Gehara *et al.* 2013; Magalhães *et al.* 2014). Consequently, climate can also influence population dynamics such as population expansion, rapid range contraction or local extinction (e.g. Carnaval *et al.* 2009;

Gehara *et al.* 2013; Magalhães *et al.* 2014). The retention of niche-related ecological traits over time (i.e. niche conservatism) may explain why species fail to disperse between different climates and habitats (Wiens *et al.* 2010; Pyron *et al.* In press). We found that the spatial distribution of genetic diversity in *C. ocellifer* is mainly associated with the distribution of suitable climates. Multiple factors can explain higher genetic diversity in areas with high suitability. First, suitable areas may maximize population fitness, and hence promote the accumulation of genetic variability (Nagaraju *et al.* 2013). Second, suitable areas may shelter large population size and retain higher genetic diversity (Gugger *et al.* 2013). Third, suitable areas may also receive regularly immigrants from neighboring unsuitable areas, increasing its intraspecific diversity. Alternatively, these assumptions are consistent with the expectation that genetic diversity would be lost more slowly in populations that occur in suitable areas. It is likely that suitable areas present lower extinction rate when compared to unsuitable areas. Hence, populations with repeated local extinctions contain lower genetic diversity (Berendonk *et al.* 2009). We hypothesized that any of such mechanisms may have favored the accumulation of *C. ocellifer* genetic diversity in suitable areas.

Isothermality and temperature seasonality are the most important variables explaining the distribution of suitable conditions for *C. ocellifer*. Although temperature oscillation intuitively denotes a constraining condition that could sustain fluctuating/unstable populations, in our study it represents the most favorable climate for *C. ocellifer* and is positively associated with the spatial distribution of its genetic diversity. Temperature is one of the most important variables that explain species richness gradients of reptiles, particularly lizards (Hawkins *et al.* 2003; Rodríguez *et al.* 2005; De Oliveira & Diniz-Filho 2010), possibly because they are ectotherms with a complex array of physiological and behavioral mechanisms for thermoregulation (Pianka & Vitt 2003). Temperature variation seems to have a positive influence on reptile richness patterns in the Caatinga (De Oliveira & Diniz-Filho

2010). Our results show that temperature oscillation can also have influenced diversity in intraspecific genetic level since localities with higher temperature variability present higher levels of genetic diversity. Evidences suggest that higher temperatures lead to faster mutation rates (Rohde 1992; Allen *et al.* 2002), but it is still not clear how temperature oscillation could increase genetic diversity. Further refined investigation is needed to clarify whether temperature variability can directly increase the genetic diversification rates in *C. ocellifer* (e.g. through increase mutation rates) or it simply translate the best climatic conditions for this species (i.e. more suitable niche).

Climatic stability has been frequently associated with high levels of genetic diversity (Carnaval *et al.* 2009; Gugger *et al.* 2013). However, some studies have not found this association (e.g. Thomé *et al.* 2010; Werneck *et al.* 2012) or found an opposite pattern, with genetic diversity negatively associated with areas of stability (e.g. Ortego *et al.* 2012; Santos *et al.* 2014). Our results show that genetic diversity in *C. ocellifer* is associated to LGM climate conditions, suggesting that effects of past climate on genetic variation can persist for many generations. This is probably related to a delayed genetic response since changes in landscape features may occur so rapidly that a considerable time lag may exist between causal events and biological response (Anderson *et al.* 2010). For instance, current patterns of genetic structure and diversity have been often explained by past environmental conditions (Anderson *et al.* 2010; e.g. Ortego *et al.* 2012; Gugger *et al.* 2013). The temporal lag is particularly remarkable for organisms with large effective population sizes (Excoffier 2004), where genetic effects may require a long time to appear (Anderson *et al.* 2010). Considering that *C. ocellifer* presents large effective population (see Oliveira *et al.* In prep), the delayed genetic responses are even more plausible. Other possible explanation may be related to influence of LGM climate-mediated demographic responses (Gugger *et al.* 2013), which is consistent with the demographic expansion experienced by *C. ocellifer* during the late

Pleistocene (see Oliveira *et al.* In prep). Investigating genetic variation of other endemic Caatinga species and which process have driven these genetic patterns may reveal common biotic responses to past climatic conditions in Caatinga.

*Cnemidophorus* lizards presents high values of body temperature and rely on sun exposure for thermoregulation (Vitt 1995; Mesquita & Colli 2003b; Dias & Rocha 2004; Menezes *et al.* 2011). It is possible that the reduced availability of direct sunlight during the rainy season decreases activities such as courtship and mating (Mesquita & Colli 2003a). This could explain the lower *C. ocellifer* genetic diversity in localities with high annual precipitation. Generally, rainier localities tend to present more cloudy days, which could result in lower reproductive rates, and ultimately in lower genetic diversity. Likewise, precipitation seems to have a negative influence on reptile richness patterns in Caatinga, with driest places harboring more reptile species than wettest places (De Oliveira & Diniz-Filho 2010). Apparently, tenuous variation of precipitation seems to have a great influence on different levels of diversity in Caatinga lizards.

The hypothesis of colonization also did not explain the spatial distribution of genetic diversity in *C. ocellifer*, probably due to a non-uniform colonization process or because of recent events that lead to genetic impoverishment in localities close to the center of origin. However, the center of origin for *C. ocellifer* genetic diversity coincides with the largest patch of high diversity (see also Oliveira *et al.* In prep). Such congruence suggests that populations located in the center of origin have persisted over time allowing diversity to accumulate. Areas close to *C. ocellifer* center of origin were also recognized as center of origin for other species in different taxa such as frogs (São Pedro *et al.* unpublished data), rodents (Nascimento *et al.* 2013), and lizards (Werneck *et al.* 2015), attesting the importance of this region as a putative center of origin for many species in the Caatinga. Investigating the probable association between these Caatinga species with their colonization history may

provide information regarding significant historical events that have a common influence on many species. Historical contributions as those revealed here (i.e. LGM climate and center of origin) show the need to consider the temporal scale in landscape-genetic studies of gene flow for a comprehensive understanding of observed genetic variation (Anderson *et al.* 2010).

#### *Isolation by distance versus isolation by resistance*

Our analyses supported increasing genetic distance with geographic distance. However, landscape features such as rivers and niche suitability added significance to the observed genetic pattern. Therefore, both patterns of IBD and isolation by resistance (IBR) influence genetic differentiation in *C. ocellifer*. IBD is especially common among ectothermic animals, suggesting a metabolic basis underlying gene flow rates (Jenkins *et al.* 2010). Ectotherms must modulate activity and location based on external temperatures, and hence, they are necessarily constrained to disperse within strict temperature limits and temporal windows of opportunity (Janzen 1967; Ghalambor *et al.* 2006). Although our results suggest that dispersal in *C. ocellifer* seems to be influenced by temperature, it is possible that temperature seasonality is an indirect measure of habitat quality. There is evidence that variation in habitat quality drive differential dispersal and hence population differentiation (Garant *et al.* 2005).

Local adaptations can also increase genetic distances among populations experiencing differences in niche suitability. In this case, reduced gene flow may reflect selection against nonlocal genotypes (Ortego *et al.* 2012; Gugger *et al.* 2013). Such assertions may explain why populations located along *C. ocellifer* range boundaries present disproportionately higher levels of genetic differentiation. Some of these genetically differentiated populations are located along the coastline, where Caatinga is replaced by Atlantic Rain Forest. This dramatic change in the landscape likely imposes selective pressures different from those present in the

typical Caatinga biome. Future studies with appropriate sampling design could explicitly test this hypothesis.

Rivers have been identified as important phylogeographic breaks in several lizards' species (e.g. Pellegrino *et al.* 2005; Torres-Pérez *et al.* 2007; Jackson & Austin 2010). The longest perennial river in the Caatinga biome, the São Francisco River (SFR), has been considered a potential barrier to gene flow for many species, including rodents (Nascimento *et al.* 2011; Nascimento *et al.* 2013) and lizards (Passoni *et al.* 2008; Siedschlag *et al.* 2010; Werneck *et al.* 2015). However, some widespread lineages in the Caatinga do not show genetic differentiation on either side of the SFR such as snakes (*Bothrops*, Machado *et al.* 2014), frogs (*Dermatonotus*, São Pedro *et al.* unpublished data), and lizards (*Vanzosaura*, Recoder *et al.* 2014; and *Phyllopezus*, Werneck *et al.* 2012). *Cnemidophorus ocellifer* also does not show any deep genetic structure at the SFR (Oliveira *et al.* In prep). However, we identified that the network of Caatinga rivers have played an important role at finer level of genetic differentiation in *C. ocellifer*, suggesting that rivers provides enough resistance to reduce gene flow among populations.

## **Conclusion**

Our results constitute a first approach on genetic variation drivers in the Caatinga, especially considering a sampling effort that covers the entire distribution of *Cnemidophorus ocellifer*. We are aware that the use of a single gene limits the interpretation of our results. Adding more loci could reinforce the genetic patterns we have found as well as identify eventual influences of factors that cannot be detected through matrilineal heritage only.

Our results indicate that landscape and environmental features are important to explain the observed patterns of genetic variation in whiptail lizard *C. ocellifer*. Our findings also reveal much about the conditions necessary for its population persistence under Caatinga

biome. Overall, genetic variation in *C. ocellifer* has been influenced mainly by temperature variability that seems to modulate gene flow rates among populations. Past environmental conditions were important in shaping the currently observed genetic diversity, suggesting a time lag in genetic response. Genetic differentiation patterns in *C. ocellifer* were explained by both isolation by distance and isolation by resistance (differences in niche suitability and main rivers). *Cnemidophorus ocellifer* is a widespread species and is currently considered as non-threatened. However, due to the key role of temperature conditions in defining its distribution range and genetic variation, it is crucial for conservation purposes to investigate how current climatic changes may affect this species in the next decades. ENM approaches that take into account putative scenarios of global warming can answer this question and also suggest conservation plans for preventing severe population declines and loss of genetic variation in *C. ocellifer*.

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### Author contributions

E.F.O. and G.C.C. conceived the initial idea of the study. E.F.O., V.A.S.P., D.O.M., A.A.G., and G.R.C. collected the samples. E.F.O. and V.A.S.P. generated the sequence data. E.F.O., P.M., V.A.S.P., and M.G. performed the analyses. All authors contributed to writing paper.

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1 **Tables and Figures**

2

3 Table 1. Genetic statistics for the sampling localities of *Cnemidophorus ocellifer*. Number of sampled individuals (N), nucleotide diversity ( $\pi$ ),  
4 haplotype diversity ( $Hd$ ), and number of haplotypes ( $H$ ). Localities and haplotypes network can be visualized in Fig. 1.

5

Map Code	Localities	State	N	$\pi$	$Hd$	$H$	Haplotypes
1	Batalha	PI	6	0.00462	0.8667	4	H1, H2(2), H3(2), H4
2	PARNA das Sete Cidades	PI	15	0.00071	0.2571	3	H1(13), H2, H55
3	São João da Fronteira	PI	6	0.00373	0.8667	4	H2(2), H76(2), H77, H78
4	Santa Quitéria	CE	12	0.00222	0.4545	4	H31(9), H82, H83, H84
5	São Gonçalo do Amarante	CE	4	0.00311	0.8333	3	H11, H74, H75(2)
6	Caucaia	CE	5	0.00267	0.8000	3	H10(2), H11(2), H12
7	Galinhos	RN	10	0.00160	0.5333	4	H2(7), H8, H35, H36
8	São Bento do Norte	RN	6	0.00142	0.5333	2	H2(4), H8(2)
9	João Câmara	RN	12	0.00178	0.5758	5	H2(8), H8, H41, H42, H43
10	Parnamirim	RN	16	0	0	1	H2(16)
11	Barra do Cunhau	RN	9	0.00059	0.2222	2	H2, H5(8)
12	Caicó	RN	6	0.00089	0.3333	2	H2(5), H13
13	Sumé	PB	5	0.00107	0.4000	2	H2(4), H31
14	Caruaru	PE	6	0.00284	0.8000	3	H2(2), H11(2), H14(2)
15	PARNA do Catimbau	PE	5	0.00160	0.6000	2	H2(3), H43(2)
16	Palmeira dos Índios	AL	7	0	0	1	H54(7)
17	Canindé de São Francisco	SE	6	0.00178	0.6000	3	H32(4), H33, H34
18	Poço Redondo	SE	7	0.00457	0.5238	3	H32(5), H56, H57
19	Nossa Senhora da Glória	SE	4	0.00133	0.5000	2	H39(3), H48
20	Santo Amaro das Brotas	SE	7	0	0	1	H73(7)
21	Conde	BA	5	0.00160	0.6000	2	H6(3), H30(2)
22	Barra do Itariri	BA	5	0.00107	0.4000	2	H6(4), H7
23	Praia do Forte	BA	6	0	0	1	H6(6)
24	Busca Vida	BA	5	0	0	1	H9(5)
25	Itaberaba	BA	4	0.00133	0.5000	2	H37(3), H38
26	Lençóis	BA	4	0	0	1	H44(4)

27	Mairi	BA	6	0.00178	0.3333	2	H37(5), H45
28	Itiúba	BA	12	0.00836	0.7121	4	H6(3), H37(2), H39(6), H40(1)
29	Tucano	BA	5	0.00800	0.8000	3	H6(2), H39(2), H88
30	EE Raso da Catarina	BA	14	0.00267	0.7692	8	H39(7), H62, H63, H64, H65, H66, H67, H68
31	Belém do São Francisco	PE	5	0.00213	0.7000	3	H1, H2(3), H8
32	Serra Talhada	PE	5	0.00107	0.4000	2	H2(4), H85
33	Salgueiro	PE	5	0.00107	0.4000	2	H2(4), H72
34	FLONA Chapada do Araripe	CE	10	0.00053	0.2000	2	H2(9), H31
35	Nova Olinda	CE	6	0.00373	0.7333	3	H2(3), H31, H47(2)
36	Tauá	CE	4	0.00400	0.8333	3	H31(2), H86, H87
37	Picos	PI	5	0.00160	0.6000	2	H31(3), H53(2)
38	Trindade	PE	4	0	0	1	H25(4)
39	Nascente	PE	4	0.01067	0.5000	2	H25, H46(3)
40	Simplício Mendes	PI	7	0.00356	0.8095	4	H16(3), H79(2), H80, H81
41	Capitão Gervásio de Oliveira	PI	10	0.00409	0.8444	6	H15, H16(4), H17, H18, H19(2), H20
42	Casa Nova	BA	9	0.00889	0.8056	5	H25(2), H26, H27(4), H28, H29
43	Petrolina	PE	14	0.00223	0.6813	6	H25, H27(8), H49, H50(2), H51, H52
44	Remanso	BA	6	0.00836	0.8000	4	H22(3), H69, H70, H71
45	Coronel José Dias	PI	7	0.00356	0.8095	4	H21(2), H22(3), H23, H24
46	PARNA Serra da Capivara	PI	15	0.00533	0.8476	7	H16, H21, H22(5), H58, H59(3), H60, H61(3)

6 National Park (PARNA), Ecological Station (EE), and National Forest (FLONA).

7 Table 2. General hypotheses tested to explain genetic diversity and structure in  
 8 *Cnemidophorus ocellifer*.  
 9

	<b>Hypothesis</b>	<b>Variables used to test</b>
<b>Genetic Diversity</b>	Niche suitability	Niche suitability (current and LGM) Bio3, Bio4, and Bio6 (current and LGM)
	Niche stability	Refugia
	Water and energy availability	Bio1, Bio12, AET, and NPP
	Environmental heterogeneity	Topographic complexity (derived from altitude)
	Colonization	Geographical distance of each locality to the CO
	<b>Hypothesis</b>	<b>Variables used to test</b>
<b>Genetic Structure</b>	Geographical distance	Euclidean geographical distances between localities
	Current niche connectivity	Current niche suitability
	LGM niche connectivity	Niche suitability during LGM
	Resistance of slope	Slope (derived from altitude)
	Resistance of roughness	Roughness (derived from altitude)
	Resistance of rivers	Main perennial rivers

10 Isothermality (Bio3), temperature seasonality (Bio4), minimum temperature of coldest month  
 11 (Bio6), annual mean temperature (Bio1), annual precipitation (Bio12), actual  
 12 evapotranspiration (AET), net primary productivity (NPP), and center of origin (CO).



13 Table 3. Percent contribution and permutation importance of each climatic variable used in  
 14 ecological niche modelling for *Cnemidophorus ocellifer*.  
 15

<b>VC</b>	<b>Variable Name</b>	<b>PC</b>	<b>PI</b>
Bio4	Temperature Seasonality (standard deviation *100)	21.1	39.7
Bio3	Isothermality (Bio2/Bio7) (* 100)	5.5	18.5
Bio6	Min Temperature of Coldest Month	21.4	14.9
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	17.5	7.5
Bio15	Precipitation Seasonality (Coefficient of Variation)	7.9	5.6
Bio19	Precipitation of Coldest Quarter	8.2	4.3
Bio12	Annual Precipitation	13.4	3.4
Bio17	Precipitation of Driest Quarter	1.9	3.3
Bio5	Max Temperature of Warmest Month	1.4	1.1
Bio18	Precipitation of Warmest Quarter	1.3	0.9
Bio8	Mean Temperature of Wettest Quarter	0.6	0.8

16 Variable code (VC), temperature annual range (Bio7), percent contribution (PC), and percent  
 17 importance (PI).

18 Table 4. Results of the linear regression or simultaneous autoregression analyses performed to test the genetic diversity in *Cnemidophorus*  
 19 *ocellifer*. The best models are highlighted in bold.  
 20

Hypothesis	Variables	Best Model	SA	F	R <sup>2</sup>	P	AIC	ΔAIC
Niche suitability	Current	Current	Yes	0.004	<0.001	0.868	-407.668	19.7
	LGM	LGM	Yes	0.228	0.005	0.736	-407.901	19.6
	Bio3C + Bio4C + Bio6C	Bio3C + Bio4C	No	8.606	0.270	<0.001	-424.161	3.3
	Bio3L + Bio4L + Bio6L	<b>Bio3L + Bio4L</b>	<b>No</b>	<b>10.848</b>	<b>0.320</b>	<b>&lt;0.001</b>	<b>-427.465</b>	<b>0</b>
Niche stability	Refugia	Refugia	Yes	0.678	0.015	0.386	-408.367	19
Water and energy availability	Bio1 + Bio12 + AET + NPP	Bio12	Yes	7.42	0.144	0.036	-414.834	12.6
Environmental heterogeneity	TCI	TCI	Yes	0.150	0.003	0.609	-407.820	19.6
Colonization	DCO	DCO	Yes	5.451	0.111	0.22	-413.036	14.4
Multiple hypotheses	All	<b>Bio3L + Bio4C</b>	<b>No</b>	<b>10.78</b>	<b>0.319</b>	<b>&lt;0.001</b>	<b>-427.369</b>	<b>0.1</b>

21 Isothermality (Bio3), temperature seasonality (Bio4), minimum temperature of coldest month (Bio6), annual mean temperature (Bio1), annual  
 22 precipitation (Bio12), actual evapotranspiration (AET), net primary productivity (NPP), topographic complexity index (TCI), and distance from  
 23 center of origin (DCO). Letters after Bio3, Bio4 and Bio6 variables represent current (C) and LGM (L) climate conditions. Evaluated parameters:  
 24 spatial autocorrelation (SA), F-statistic (F), coefficient of determination (R<sup>2</sup>), P-value (P), Akaike Information Criterion (AIC), and the difference  
 25 between AIC value and the minimum AIC for the set of models compared (ΔAIC).

26 Table 5. Results of the multiple regressions on distance matrices (MRM) performed to test the genetic differentiation in *Cnemidophorus ocellifer*.  
 27 The best models are highlighted in bold.  
 28

Model	Variable	Beta	R <sup>2</sup>	F	P	AIC	ΔAIC
Simple	Roughness	-0.00015	0.0002	0.198	0.8923	191.506	127.3
	NSLGM	0.00829	0.0081	8.423	0.3980	183.299	119.0
	Slope	0.27871	0.0091	9.445	0.3419	182.284	118.0
	NSCURRENT	0.09024	0.0573	62.827	0.0070	130.596	66.3
	River	0.24897	0.0934	106.439	0.0012	90.203	26.0
	Geographic Distance (Geog. Dist.)	0.03942	0.0935	106.557	< 0.001	90.096	25.8
Multiple	Geog. Dist. + NSCURRENT	-	0.0951	54.227	0.0022	90.279	26.0
	River + NSCURRENT	-	0.1130	65.730	0.0014	69.608	5.4
	<b>Geog. Dist. + River</b>	-	<b>0.1160</b>	<b>67.697</b>	<b>&lt; 0.001</b>	<b>66.114</b>	<b>1.9</b>
	<b>Geog. Dist. + River + NSCURRENT</b>	-	<b>0.1193</b>	<b>46.541</b>	<b>0.0017</b>	<b>64.253</b>	<b>0</b>

29 Evaluated parameters: beta, coefficient of determination (R<sup>2</sup>), F-statistic (F), P-value (P), Akaike Information Criterion (AIC), and the difference  
 30 between AIC value and the minimum AIC for the set of models compared (ΔAIC).

Fig. 1. Map with localities sampled for genetic data of the whiptail lizard *Cnemidophorus ocellifer* along the Caatinga biome (light gray). Haplotypes genealogy from Maximum Likelihood analysis of the 12S gene tree performed in the software Haploviewer. Each haplotype is represented by a circle whose size is proportional to its frequency (indicated in legend). The localities where each haplotype (coded as a number) occurs are available in Table 1.

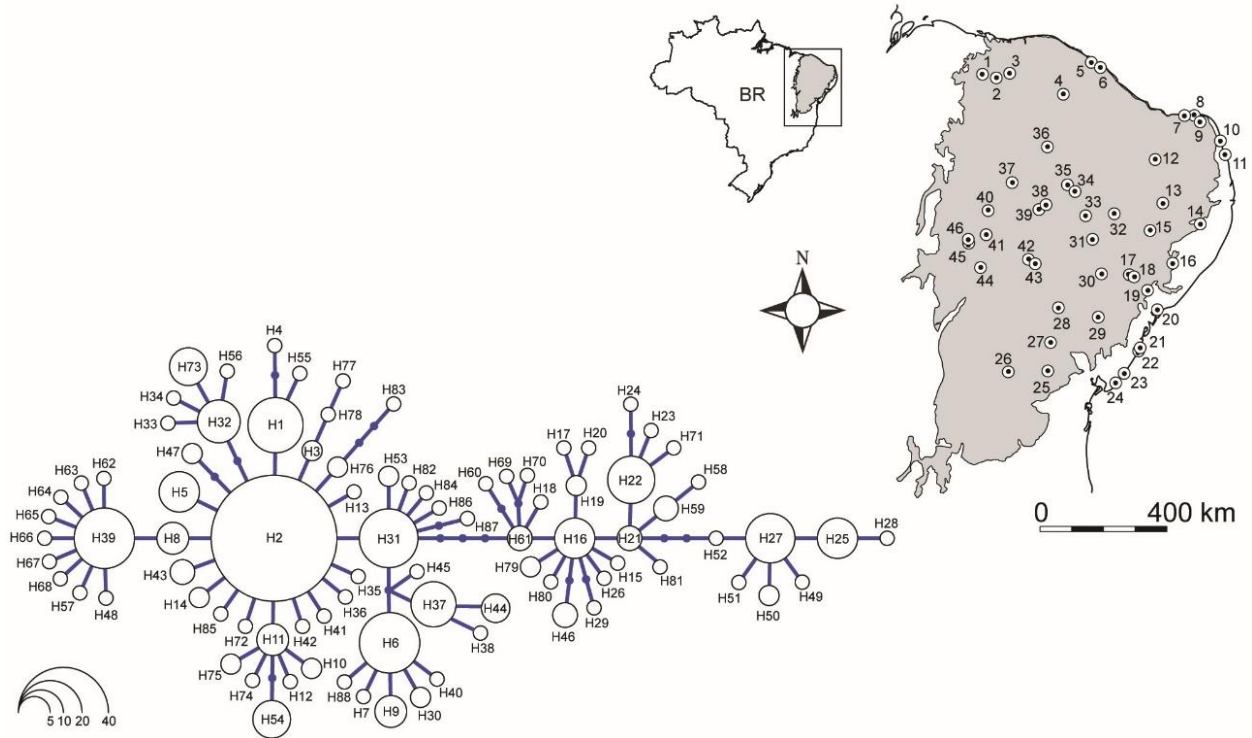


Fig. 2. Spatial distribution of the genetic variation in *Cnemidophorus ocellifer* represented by interpolated  $\pi$  values (A) and interpolated pairwise genetic distance (B).

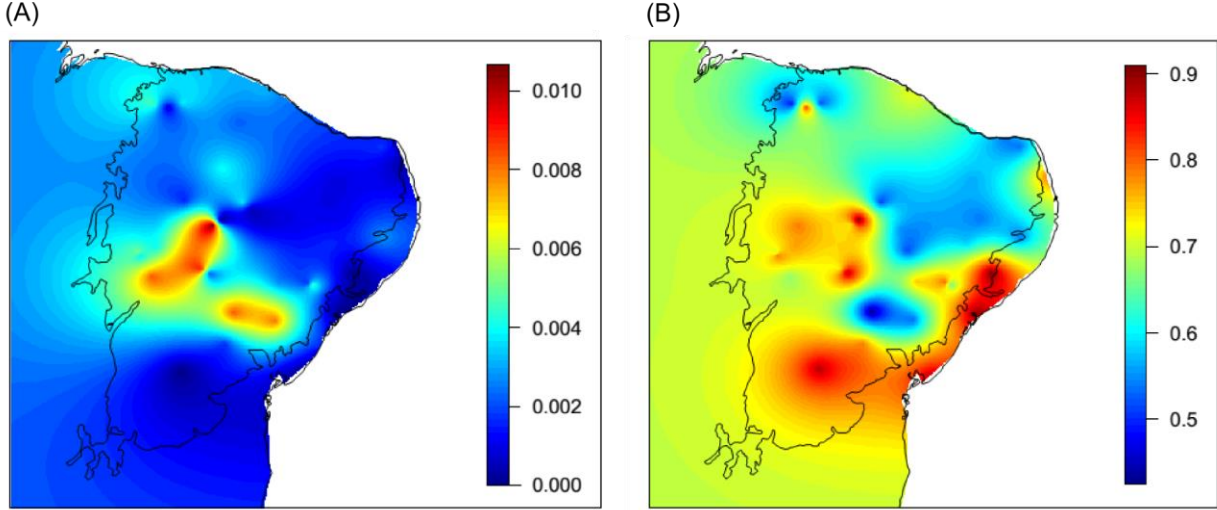
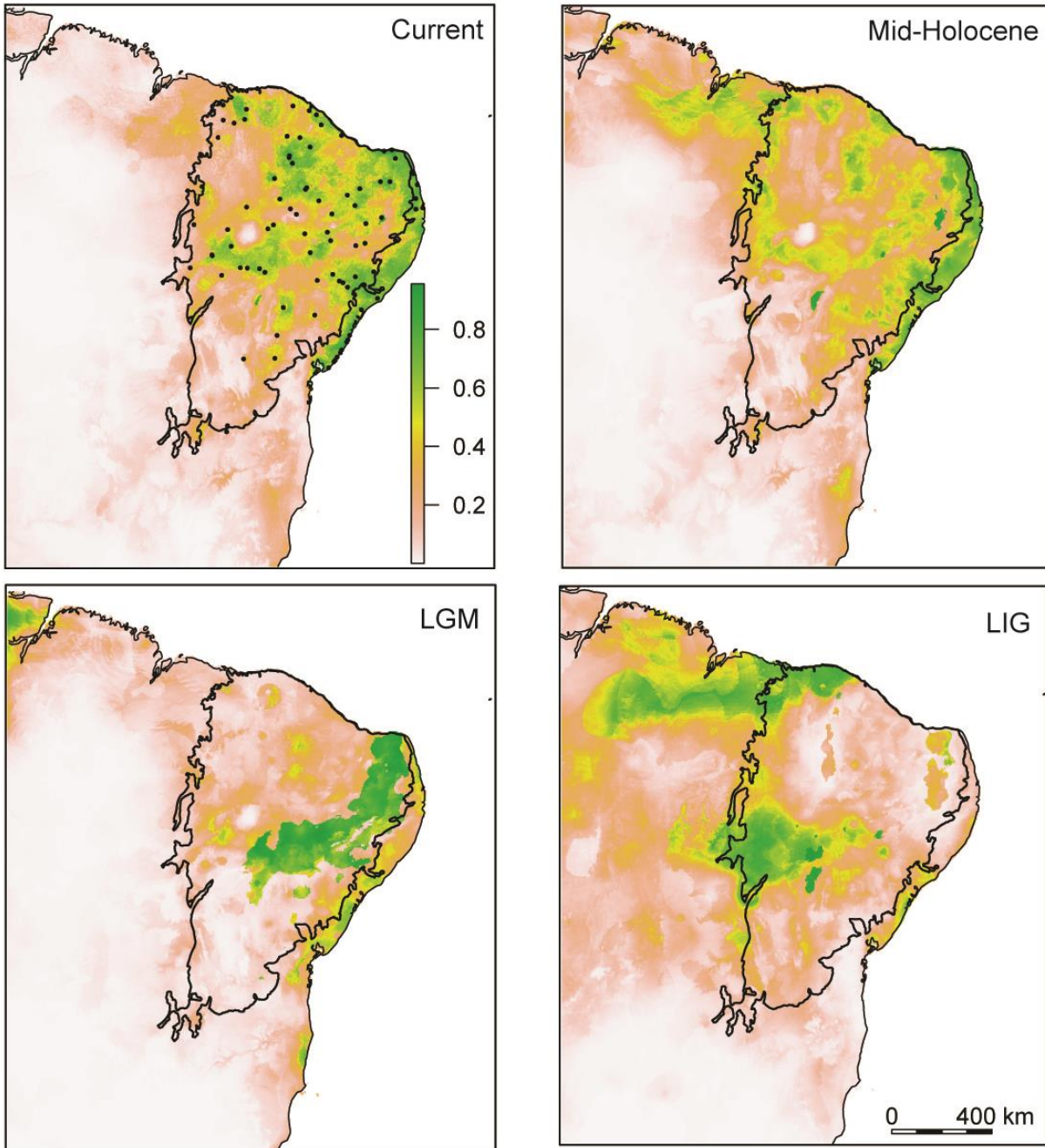


Fig. 3. Geographic distribution of climatically suitable habitats for *Cnemidophorus ocellifer* during four temporal scenarios: current, mid-Holocene (6 kyr), Last Glacial Maximum (LGM, 21 kyr) and Last Interglacial (LIG, ~130 kyr). Black dots represent all 91 localities (available at Table S3, Supporting information) used as species occurrence dataset in niche modelling procedures.



## Supporting information

### Tables and Figures

Table S1. Samples of *Cnemidophorus ocellifer* used in present study (336 samples). A map code number (see Fig. 1) is presented for each sample, along with locality, state, institution of origin, voucher number, laboratorial code number, and geographic coordinates (longitude and latitude in decimal degrees).

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
1	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO73	N105	-42.1042	-3.9974
1	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO74	N108	-42.1042	-3.9974
1	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO75	N103	-42.1042	-3.9974
1	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO76	N104	-42.1042	-3.9974
1	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO78	N106	-42.1042	-3.9974
1	<i>Cnemidophorus ocellifer</i>	Batalha	PI	UFRN	EFO79	N109	-42.1042	-3.9974
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60733	N7	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60734	N8	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60735	N9	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60736	N10	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60737	N11	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60738	N12	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60739	N13	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60740	N14	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60742	N16	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60743	N17	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60747	N18	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60748	N19	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60749	N20	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60750	N21	-41.7083	-4.1014
2	<i>Cnemidophorus ocellifer</i>	PARNA das Sete Cidades	PI	UnB	CHUNB60751	N22	-41.7083	-4.1014
3	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO82	N113	-41.323	-3.9692

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
3	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO83	N117	-41.323	-3.9692
3	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO84	N118	-41.323	-3.9692
3	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO86	N112	-41.323	-3.9692
3	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO87	N114	-41.323	-3.9692
3	<i>Cnemidophorus ocellifer</i>	São João da Fronteira	PI	UFRN	EFO88	N116	-41.323	-3.9692
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB382	N394	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB406	N406	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB439	N393	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB540	N395	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB550	N397	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB832	N398	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB833	N399	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB965	N400	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB980	N402	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB990	N403	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB993	N405	-39.7793	-4.5715
4	<i>Cnemidophorus ocellifer</i>	Santa Quitéria	CE	UFPB	FSCHUFPB994	N407	-39.7793	-4.5715
5	<i>Cnemidophorus ocellifer</i>	São Gonçalo do Amarante	CE	UFRN	EFO50	N84	-38.9736	-3.6568
5	<i>Cnemidophorus ocellifer</i>	São Gonçalo do Amarante	CE	UFRN	EFO53	N86	-38.9736	-3.6568
5	<i>Cnemidophorus ocellifer</i>	São Gonçalo do Amarante	CE	UFRN	EFO54	N81	-38.9736	-3.6568
5	<i>Cnemidophorus ocellifer</i>	São Gonçalo do Amarante	CE	UFRN	EFO55	N85	-38.9736	-3.6568
6	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec3159	N528	-38.7113	-3.8041
6	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec3175	N529	-38.7113	-3.8041
6	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec3210	N530	-38.7113	-3.8041
6	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec941	N522	-38.7113	-3.8041
6	<i>Cnemidophorus ocellifer</i>	Caucaia	CE	UFC	Tec942	N523	-38.7113	-3.8041
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC10	N502	-36.2486	-5.1042
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC11	N503	-36.2486	-5.1042
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC16	N506	-36.2486	-5.1042
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC2	N509	-36.2486	-5.1042



Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC3	N510	-36.2486	-5.1042
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC4	N511	-36.2486	-5.1042
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC6	N504	-36.2486	-5.1042
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC7	N505	-36.2486	-5.1042
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC8	N507	-36.2486	-5.1042
7	<i>Cnemidophorus</i> sp.	Galinhos	RN	UFPB	MC9	N508	-36.2486	-5.1042
8	<i>Cnemidophorus ocellifer</i>	São Bento do Norte	RN	UFRN	AAGARDA3641	N291	-35.9659	-5.0631
8	<i>Cnemidophorus ocellifer</i>	São Bento do Norte	RN	UFRN	AAGARDA5838	N350	-35.9659	-5.0631
8	<i>Cnemidophorus ocellifer</i>	São Bento do Norte	RN	UFRN	SB6	N381	-35.9659	-5.0631
8	<i>Cnemidophorus ocellifer</i>	São Bento do Norte	RN	UFRN	SB7	N382	-35.9659	-5.0631
8	<i>Cnemidophorus ocellifer</i>	São Bento do Norte	RN	UFRN	SB8	N383	-35.9659	-5.0631
8	<i>Cnemidophorus ocellifer</i>	São Bento do Norte	RN	UFRN	SB12	N385	-35.9659	-5.0631
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	AAGARDA5601	N334	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	AAGARDA5605	N331	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	AAGARDA5606	N332	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	AAGARDA5607	N333	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	AAGARDA5611	N336	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	AAGARDA5613	N337	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	AAGARDA5621	N339	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	AAGARDA5622	N340	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	AAGARDA5775	N346	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFPB	FSCHUFPB2510	N445	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFPB	FSCHUFPB2541	N448	-35.8393	-5.3651
9	<i>Cnemidophorus ocellifer</i>	João Câmara	RN	UFRN	MV15	N377	-35.8393	-5.3651
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA3529	N289	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6036	N355	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6037	N356	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6063	N357	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6064	N358	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6070	N359	-35.1764	-5.9122

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10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6071	N360	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6072	N361	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6073	N362	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6074	N363	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6088	N364	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6112	N366	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6105	N367	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6107	N369	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6114	N371	-35.1764	-5.9122
10	<i>Cnemidophorus ocellifer</i>	Parnamirim	RN	UFRN	AAGARDA6121	N372	-35.1764	-5.9122
11	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2052	N434	-35.0397	-6.3072
11	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2053	N421	-35.0397	-6.3072
11	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2055	N422	-35.0397	-6.3072
11	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2064	N424	-35.0397	-6.3072
11	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2065	N429	-35.0397	-6.3072
11	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2319	N430	-35.0397	-6.3072
11	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2320	N435	-35.0397	-6.3072
11	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2323	N438	-35.0397	-6.3072
11	<i>Cnemidophorus ocellifer</i>	Barra do Cunhau	RN	UFPB	FSCHUFPB2326	N440	-35.0397	-6.3072
12	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO11	N47	-37.1346	-6.4482
12	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO13	N48	-37.1346	-6.4482
12	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO14	N49	-37.1346	-6.4482
12	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO6	N51	-37.1346	-6.4482
12	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO7	N53	-37.1346	-6.4482
12	<i>Cnemidophorus ocellifer</i>	Caicó	RN	UFRN	EFO8	N54	-37.1346	-6.4482
13	<i>Cnemidophorus ocellifer</i>	Sumé	PB	UFRN	EFO95	N123	-36.914	-7.6985
13	<i>Cnemidophorus ocellifer</i>	Sumé	PB	UFRN	EFO96	N124	-36.914	-7.6985
13	<i>Cnemidophorus ocellifer</i>	Sumé	PB	UFRN	EFO97	N125	-36.914	-7.6985
13	<i>Cnemidophorus ocellifer</i>	Sumé	PB	UFRN	EFO98	N126	-36.914	-7.6985
13	<i>Cnemidophorus ocellifer</i>	Sumé	PB	UFRN	EFO99	N127	-36.914	-7.6985

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
14	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO191	N208	-35.8364	-8.2986
14	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO192	N204	-35.8364	-8.2986
14	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO194	N205	-35.8364	-8.2986
14	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO195	N209	-35.8364	-8.2986
14	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN	EFO197	N211	-35.8364	-8.2986
14	<i>Cnemidophorus ocellifer</i>	Caruaru	PE	UFRN		N206		
15	<i>Cnemidophorus ocellifer</i>	PARNA do Catimbau	PE	USP	MRT14118	N732	-37.2812	-8.4871
15	<i>Cnemidophorus ocellifer</i>	PARNA do Catimbau	PE	USP	MRT15363	N734	-37.2812	-8.4871
15	<i>Cnemidophorus ocellifer</i>	PARNA do Catimbau	PE	USP	MRT15369	N735	-37.2812	-8.4871
15	<i>Cnemidophorus ocellifer</i>	PARNA do Catimbau	PE	USP	MRT15698	N737	-37.2812	-8.4871
15	<i>Cnemidophorus ocellifer</i>	PARNA do Catimbau	PE	USP	MRT15699	N738	-37.2812	-8.4871
16	<i>Cnemidophorus ocellifer</i>	Palmeira dos Índios	AL	UFRN	EFO256	N256	-36.6283	-9.4241
16	<i>Cnemidophorus ocellifer</i>	Palmeira dos Índios	AL	UFRN	EFO257	N257	-36.6283	-9.4241
16	<i>Cnemidophorus ocellifer</i>	Palmeira dos Índios	AL	UFRN	EFO259	N259	-36.6283	-9.4241
16	<i>Cnemidophorus ocellifer</i>	Palmeira dos Índios	AL	UFRN	EFO260	N260	-36.6283	-9.4241
16	<i>Cnemidophorus ocellifer</i>	Palmeira dos Índios	AL	UFRN	EFO261	N261	-36.6283	-9.4241
16	<i>Cnemidophorus ocellifer</i>	Palmeira dos Índios	AL	UFRN	EFO262	N262	-36.6283	-9.4241
16	<i>Cnemidophorus ocellifer</i>	Palmeira dos Índios	AL	UFRN	EFO263	N263	-36.6283	-9.4241
17	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A129	N459	-37.8769	-9.7567
17	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A135	N460	-37.8769	-9.7567
17	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A144	N463	-37.8769	-9.7567
17	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A145	N464	-37.8769	-9.7567
17	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	A67	N451	-37.8769	-9.7567
17	<i>Cnemidophorus ocellifer</i>	Canindé de São Francisco	SE	UFPB	FSCHUFPB291	N392	-37.8769	-9.7567
18	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A117	N455	-37.7439	-9.8168
18	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A148	N457	-37.7439	-9.8168
18	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A149	N465	-37.7439	-9.8168
18	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A151	N466	-37.7439	-9.8168
18	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A73	N468	-37.7439	-9.8168
18	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A89	N453	-37.7439	-9.8168

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18	<i>Cnemidophorus ocellifer</i>	Poço Redondo	SE	UFPB	A93	N456	-37.7439	-9.8168
19	<i>Cnemidophorus ocellifer</i>	Nossa Senhora da Glória	SE	UFPB	L133	N495	-37.3537	-10.205
19	<i>Cnemidophorus ocellifer</i>	Nossa Senhora da Glória	SE	UFPB	L136	N497	-37.3537	-10.205
19	<i>Cnemidophorus ocellifer</i>	Nossa Senhora da Glória	SE	UFPB	L149	N496	-37.3537	-10.205
19	<i>Cnemidophorus ocellifer</i>	Nossa Senhora da Glória	SE	UFPB	L150	N498	-37.3537	-10.205
20	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12567	N724	-37.0717	-10.788
20	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12569	N723	-37.0717	-10.788
20	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12570	N725	-37.0717	-10.788
20	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12571	N726	-37.0717	-10.788
20	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12572	N727	-37.0717	-10.788
20	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12573	N728	-37.0717	-10.788
20	<i>Cnemidophorus ocellifer</i>	Santo Amaro das Brotas	SE	USP	MRT12574	N729	-37.0717	-10.788
21	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO269	N277	-37.568	-11.857
21	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO270	N280	-37.568	-11.857
21	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO271	N278	-37.568	-11.857
21	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO272	N279	-37.568	-11.857
21	<i>Cnemidophorus ocellifer</i>	Conde	BA	UFRN	EFO273	N281	-37.568	-11.857
22	<i>Cnemidophorus ocellifer</i>	Barra do Itariri	BA	UCSAL	CHECOA2446	N543	-37.6107	-11.945
22	<i>Cnemidophorus ocellifer</i>	Barra do Itariri	BA	UCSAL	CHECOA2448	N545	-37.6107	-11.945
22	<i>Cnemidophorus ocellifer</i>	Barra do Itariri	BA	UCSAL	CHECOA2551	N558	-37.6107	-11.945
22	<i>Cnemidophorus ocellifer</i>	Barra do Itariri	BA	UCSAL	CHECOA2553	N559	-37.6107	-11.945
22	<i>Cnemidophorus ocellifer</i>	Barra do Itariri	BA	UCSAL	CHECOA-A8	N569	-37.6107	-11.945
23	<i>Cnemidophorus ocellifer</i>	Praia do Forte	BA	UCSAL	CHECOA2470	N546	-38.0283	-12.59
23	<i>Cnemidophorus ocellifer</i>	Praia do Forte	BA	UCSAL	CHECOA2473	N548	-38.0283	-12.59
23	<i>Cnemidophorus ocellifer</i>	Praia do Forte	BA	UCSAL	CHECOA2474	N549	-38.0283	-12.59
23	<i>Cnemidophorus ocellifer</i>	Praia do Forte	BA	UCSAL	CHECOA2476	N551	-38.0283	-12.59
23	<i>Cnemidophorus ocellifer</i>	Praia do Forte	BA	UCSAL	CHECOA2477	N552	-38.0283	-12.59
23	<i>Cnemidophorus ocellifer</i>	Praia do Forte	BA	USP	MRT12557	N720	-38.0283	-12.59
24	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	A2	N563	-38.2705	-12.862
24	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	CHECOA2483	N553	-38.2705	-12.862

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24	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	CHECOA2484	N554	-38.2705	-12.862
24	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	CHECOA2486	N555	-38.2705	-12.862
24	<i>Cnemidophorus ocellifer</i>	Busca Vida	BA	UCSAL	CHECOA2488	N556	-38.2705	-12.862
25	<i>Cnemidophorus ocellifer</i>	Itaberaba	BA	UFRN	EFO198	N217	-40.2251	-12.521
25	<i>Cnemidophorus ocellifer</i>	Itaberaba	BA	UFRN	EFO199	N212	-40.2251	-12.521
25	<i>Cnemidophorus ocellifer</i>	Itaberaba	BA	UFRN	EFO200	N213	-40.2251	-12.521
25	<i>Cnemidophorus ocellifer</i>	Itaberaba	BA	UFRN	EFO203	N214	-40.2251	-12.521
26	<i>Cnemidophorus</i> sp.	Lençois	BA	USP	MTR19916	N761	-41.364	-12.546
26	<i>Cnemidophorus</i> sp.	Lençois	BA	USP	MTR19917	N762	-41.364	-12.546
26	<i>Cnemidophorus</i> sp.	Lençois	BA	USP	MTR19918	N763	-41.364	-12.546
26	<i>Cnemidophorus</i> sp.	Lençois	BA	USP	MTR19989	N764	-41.364	-12.546
27	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO228	N242	-40.1473	-11.703
27	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO229	N237	-40.1473	-11.703
27	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO230	N238	-40.1473	-11.703
27	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO231	N239	-40.1473	-11.703
27	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO232	N240	-40.1473	-11.703
27	<i>Cnemidophorus ocellifer</i>	Mairi	BA	UFRN	EFO233	N241	-40.1473	-11.703
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO235	N244	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO237	N257	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO239	N258	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO240	N246	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO241	N248	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO243	N249	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO244	N250	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO245	N252	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO246	N253	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO247	N254	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO248	N255	-39.9199	-10.704
28	<i>Cnemidophorus ocellifer</i>	Itiúba	BA	UFRN	EFO249	N256	-39.9199	-10.704
29	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO251	N260	-38.7727	-10.974

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
29	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO252	N263	-38.7727	-10.974
29	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO253	N261	-38.7727	-10.974
29	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO254	N262	-38.7727	-10.974
29	<i>Cnemidophorus ocellifer</i>	Tucano	BA	UFRN	EFO255	N264	-38.7727	-10.974
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4105	N299	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4247	N301	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4296	N309	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4297	N294	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4302	N296	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4303	N297	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4304	N298	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4307	N300	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4318	N304	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4319	N305	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4320	N306	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4321	N307	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4336	N308	-38.6828	-9.7316
30	<i>Cnemidophorus</i> sp.	EE Raso da Catarina	BA	UFRN	AAGARDA4515	N312	-38.6828	-9.7316
31	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO178	N192	-38.9372	-8.7384
31	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO180	N194	-38.9372	-8.7384
31	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO182	N196	-38.9372	-8.7384
31	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO183	N197	-38.9372	-8.7384
31	<i>Cnemidophorus ocellifer</i>	Belém do São Francisco	PE	UFRN	EFO186	N200	-38.9372	-8.7384
32	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Serra Talhada	PE	UFPB	FRD1067	N490	-38.3129	-8.0039
32	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Serra Talhada	PE	UFPB	FRD1068	N491	-38.3129	-8.0039
32	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Serra Talhada	PE	UFPB	FRD1069	N492	-38.3129	-8.0039
32	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Serra Talhada	PE	UFPB	FRD1074	N493	-38.3129	-8.0039
32	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Serra Talhada	PE	UFPB	FRD1098	N494	-38.3129	-8.0039
33	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO100	N132	-39.1366	-8.0628
33	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO102	N128	-39.1366	-8.0628

Map code	Species	Locality	State	Institution	Voucher	Lab code	Long	Lat
33	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO103	N130	-39.1366	-8.0628
33	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO104	N131	-39.1366	-8.0628
33	<i>Cnemidophorus ocellifer</i>	Salgueiro	PE	UFRN	EFO108	N136	-39.1366	-8.0628
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64550	N39	-39.4413	-7.3658
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64554	N28	-39.4413	-7.3658
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64555	N31	-39.4413	-7.3658
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64557	N32	-39.4413	-7.3658
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64558	N34	-39.4413	-7.3658
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64560	N35	-39.4413	-7.3658
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64561	N37	-39.4413	-7.3658
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64562	N38	-39.4413	-7.3658
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64564	N41	-39.4413	-7.3658
34	<i>Cnemidophorus ocellifer</i>	FLONA Chapada do Araripe	CE	UnB	CHUNB64565	N42	-39.4413	-7.3658
35	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11903	N708	-39.6601	-7.1716
35	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11905	N709	-39.6601	-7.1716
35	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11906	N710	-39.6601	-7.1716
35	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11907	N711	-39.6601	-7.1716
35	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11908	N712	-39.6601	-7.1716
35	<i>Cnemidophorus ocellifer</i>	Nova Olinda	CE	USP	MRT11909	N713	-39.6601	-7.1716
36	<i>Cnemidophorus ocellifer</i>	Tauá	CE	UFRN	EFO34	N74	-40.2368	-6.0853
36	<i>Cnemidophorus ocellifer</i>	Tauá	CE	UFRN	EFO35	N75	-40.2368	-6.0853
36	<i>Cnemidophorus ocellifer</i>	Tauá	CE	UFRN	EFO36	N72	-40.2368	-6.0853
36	<i>Cnemidophorus ocellifer</i>	Tauá	CE	UFRN	EFO37	N73	-40.2368	-6.0853
37	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO110	N138	-41.2537	-7.1085
37	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO111	N141	-41.2537	-7.1085
37	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO113	N137	-41.2537	-7.1085
37	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO114	N140	-41.2537	-7.1085
37	<i>Cnemidophorus ocellifer</i>	Picos	PI	UFRN	EFO115	N142	-41.2537	-7.1085
38	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Trindade	PE	UFPB	FRD927	N477	-40.2768	-7.7452
38	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Trindade	PE	UFPB	FRD928	N478	-40.2768	-7.7452

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38	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Trindade	PE	UFPB	FRD929	N479	-40.2768	-7.7452
38	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Trindade	PE	UFPB	FRD967	N485	-40.2768	-7.7452
39	<i>Cnemidophorus</i> <i>ocellifer</i>	Nascente	PE	UFPB	FRD941	N480	-40.4805	-7.8831
39	<i>Cnemidophorus</i> <i>ocellifer</i>	Nascente	PE	UFPB	FRD942	N481	-40.4805	-7.8831
39	<i>Cnemidophorus</i> <i>ocellifer</i>	Nascente	PE	UFPB	FRD943	N482	-40.4805	-7.8831
39	<i>Cnemidophorus</i> <i>ocellifer</i>	Nascente	PE	UFPB	FRD944	N483	-40.4805	-7.8831
40	<i>Cnemidophorus</i> <i>ocellifer</i>	Simplício Mendes	PI	UFRN	EFO119	N146	-41.9443	-7.9137
40	<i>Cnemidophorus</i> <i>ocellifer</i>	Simplício Mendes	PI	UFRN	EFO120	N150	-41.9443	-7.9137
40	<i>Cnemidophorus</i> <i>ocellifer</i>	Simplício Mendes	PI	UFRN	EFO122	N153	-41.9443	-7.9137
40	<i>Cnemidophorus</i> <i>ocellifer</i>	Simplício Mendes	PI	UFRN	EFO123	N145	-41.9443	-7.9137
40	<i>Cnemidophorus</i> <i>ocellifer</i>	Simplício Mendes	PI	UFRN	EFO124	N148	-41.9443	-7.9137
40	<i>Cnemidophorus</i> <i>ocellifer</i>	Simplício Mendes	PI	UFRN	EFO127	N149	-41.9443	-7.9137
40	<i>Cnemidophorus</i> <i>ocellifer</i>	Simplício Mendes	PI	UFRN	EFO128	N154	-41.9443	-7.9137
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV11	N582	-41.9993	-8.6079
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV12	N585	-41.9993	-8.6079
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV14	N597	-41.9993	-8.6079
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV59	N598	-41.9993	-8.6079
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV6	N600	-41.9993	-8.6079
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV62	N583	-41.9993	-8.6079
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV63	N584	-41.9993	-8.6079
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV64	N596	-41.9993	-8.6079
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV65	N599	-41.9993	-8.6079
41	<i>Cnemidophorus</i> gr. <i>ocellifer</i>	Capitão Gervásio de Oliveira	PI	USP	CGERV66	N601	-41.9993	-8.6079
42	<i>Cnemidophorus</i> <i>ocellifer</i>	Casa Nova	BA	UFRN	EFO165	N179	-40.7837	-9.3139
42	<i>Cnemidophorus</i> <i>ocellifer</i>	Casa Nova	BA	UFRN	EFO166	N180	-40.7837	-9.3139
42	<i>Cnemidophorus</i> <i>ocellifer</i>	Casa Nova	BA	UFRN	EFO167	N181	-40.7837	-9.3139
42	<i>Cnemidophorus</i> <i>ocellifer</i>	Casa Nova	BA	UFRN	EFO168	N185	-40.7837	-9.3139
42	<i>Cnemidophorus</i> <i>ocellifer</i>	Casa Nova	BA	UFRN	EFO171	N188	-40.7837	-9.3139
42	<i>Cnemidophorus</i> <i>ocellifer</i>	Casa Nova	BA	UFRN	EFO172	N182	-40.7837	-9.3139
42	<i>Cnemidophorus</i> <i>ocellifer</i>	Casa Nova	BA	UFRN	EFO174	N186	-40.7837	-9.3139



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42	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO176	N190	-40.7837	-9.3139
42	<i>Cnemidophorus ocellifer</i>	Casa Nova	BA	UFRN	EFO177	N191	-40.7837	-9.3139
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11225	N652	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11226	N657	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11227	N666	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11228	N667	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11229	N662	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11230	N663	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MTR11231	N664	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3763	N665	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3764	N668	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3765	N651	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3766	N653	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3768	N654	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3769	N655	-40.5883	-9.4428
43	<i>Cnemidophorus ocellifer</i>	Petrolina	PE	USP	MRT3770	N656	-40.5883	-9.4428
44	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO148	N177	-42.1625	-9.5503
44	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO149	N178	-42.1625	-9.5503
44	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO150	N172	-42.1625	-9.5503
44	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO152	N173	-42.1625	-9.5503
44	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO153	N174	-42.1625	-9.5503
44	<i>Cnemidophorus ocellifer</i>	Remanso	BA	UFRN	EFO154	N176	-42.1625	-9.5503
45	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO130	N156	-42.5025	-8.8478
45	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO131	N161	-42.5025	-8.8478
45	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO133	N155	-42.5025	-8.8478
45	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO135	N158	-42.5025	-8.8478
45	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO136	N160	-42.5025	-8.8478
45	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO137	N162	-42.5025	-8.8478
45	<i>Cnemidophorus ocellifer</i>	Coronel José Dias	PI	UFRN	EFO138	N163	-42.5025	-8.8478
46	<i>Cnemidophorus cf. ocellifer</i>	PARNA Serra da Capivara	PI	UFRN	AAGARDA4702	N313	-42.515	-8.8186

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46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5405	N317	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5419	N320	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5433	N321	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5439	N330	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5448	N314	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5449	N315	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5450	N316	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5466	N322	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5469	N323	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5470	N324	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5471	N325	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5473	N326	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5478	N328	-42.515	-8.8186
46	<i>Cnemidophorus</i> sp.	PARNA Serra da Capivara	PI	UFRN	AAGARDA5479	N329	-42.515	-8.8186

Institution abbreviations: Universidade de Brasília (UnB), Universidade de São Paulo (USP), Universidade Católica do Salvador (UCSAL), Universidade Federal da Paraíba (UFPB), Universidade Federal do Rio Grande do Norte (UFRN), Universidade Federal de Alagoas (UFAL), Universidade Federal de Viçosa (UFV), and Universidade Federal do Ceará (UFC); Locality abbreviations: National Park (PARNA), Ecological Station (EE), and National Forest (FLONA); State abbreviations: Alagoas (AL), Bahia (BA), Ceará (CE), Maranhão (MA), Minas Gerais (MG), Paraíba (PB), Pernambuco (PE), Piauí (PI), Rio Grande do Norte (RN), and Sergipe (SE).

Table S2. Matrix of pairwise  $F_{ST}$  distances (bellow the diagonal) and significant  $F_{ST}$  p-values (above the diagonal) for the 46 sampled localities of *Cnemidophorus ocellifer*. Available at <http://costagc.weebly.com/publications.html>.

Table S3. Occurrence dataset of *Cnemidophorus ocellifer* used in Ecological Niche Modelling. For each locality the data source and geographic coordinates (in decimal degrees) are presented.

<b>Localities</b>	<b>State</b>	<b>Data source</b>	<b>Long</b>	<b>Lat</b>
Itaberaba	BA	collector	-40.2251	-12.5213
Lençóis	BA	collector	-41.3640	-12.5457
São Gonçalo do Amarante	CE	collector	-38.9736	-3.6568
Tauá	CE	collector	-40.2368	-6.0853
Nascente	PE	collector	-40.4805	-7.8831
Trindade	PE	collector	-40.2768	-7.7452
Nossa Senhora da Glória	SE	collector	-37.3537	-10.2049
Barra do Itariri	BA	collector	-37.6107	-11.9450
Busca Vida	BA	collector	-38.2705	-12.8619
Conde	BA	collector	-37.5680	-11.8569
Caucaia	CE	Borges-Nojosa <i>et al.</i> 2010	-38.7113	-3.8041
Tucano	BA	collector	-38.7727	-10.9742
Sumé	PB	collector	-36.9140	-7.6985
Belém de São Francisco	PE	collector	-38.9372	-8.7384
PARNA do Catimbau	PE	collection data	-37.2812	-8.4871
Salgueiro	PE	collector	-39.1366	-8.0628
Serra Talhada	PE	collector	-38.3129	-8.0039
Picos	PI	collector	-41.2537	-7.1085
Mairi	BA	collector	-40.1473	-11.7031
Praia do Forte	BA	collector	-38.0283	-12.5895
Remanso	BA	collector	-42.1625	-9.5503
Nova Olinda	CE	collector	-39.6601	-7.1716
Caruaru	PE	collector	-35.8364	-8.2986
Batalha	PI	collector	-42.1042	-3.9974
São João da Fronteira	PI	collector	-41.3230	-3.9692
Caicó	RN	collector	-37.1346	-6.4482
São Bento do Norte	RN	collector	-35.9659	-5.0631
Canindé de São Francisco	SE	collector	-37.8769	-9.7567
Palmeira dos Índios	AL	collector	-36.6283	-9.4241
Coronel José Dias	PI	collector	-42.5025	-8.8478
Simplício Mendes	PI	collector	-41.9443	-7.9137
Poço Redondo	SE	collector	-37.7439	-9.8168
Santo Amaro das Brotas	SE	collector	-37.0717	-10.7875
Casa Nova	BA	collector	-40.7837	-9.3139
Barra do Cunhau	RN	collector	-35.0397	-6.3072
FLONA Chapada do Araripe	CE	collector	-39.4413	-7.3658
Capitão Gervásio de Oliveira	PI	Pavan <i>et al.</i> 2008	-41.9993	-8.6079
Galinhos	RN	collector	-36.2486	-5.1042
Itiúba	BA	collector	-39.9199	-10.7036
Santa Quitéria	CE	collector	-39.7793	-4.5715
João Câmara	RN	collector	-35.8393	-5.3651
EE Raso da Catarina	BA	collector	-38.6828	-9.7316
Petrolina	PE	collector	-40.5883	-9.4428

<b>Localities</b>	<b>State</b>	<b>Data source</b>	<b>Long</b>	<b>Lat</b>
PARNA das Setes Cidades	PI	collection data	-41.7083	-4.1014
PARNA Serra da Capivara	PI	collector	-42.5150	-8.8186
Parnamirim	RN	collector	-35.1764	-5.9122
Olho d'água das Flores	AL	collector	-37.2954	-9.6005
Piaçabuçu	AL	collector	-36.4905	-10.3746
Traipu	AL	collector	-36.9679	-9.8978
Atoleiro	BA	collector	-41.2283	-9.2911
Condeúba	BA	collection data	-41.9496	-14.9336
Itacimirim	BA	collector	-38.0764	-12.6431
Massarandupió	BA	collector	-37.8384	-12.3195
Paulo Afonso	BA	collector	-38.1172	-9.5131
Serra do Lajedo	BA	collector	-41.4831	-9.2803
Mineirolândia	CE	collector	-39.5890	-5.5392
Pacajús	CE	Borges-Nojosa <i>et al.</i> 2010	-38.5371	-4.1638
Viçosa do Ceará	CE	collection data	-41.2605	-3.6083
Cabaceiras	PB	collector	-36.3399	-7.4853
Cruz do Espírito Santo	PB	collector	-35.0925	-7.1826
Itaporanga	PB	collection data	-38.1494	-7.3534
João Pessoa	PB	collector	-34.8428	-7.1366
Rio Tinto	PB	collector	-35.0950	-6.8022
Caracol	PI	collector	-43.3068	-9.2842
Joaquim Pires	PI	collector	-42.1087	-3.4538
Nossa Senhora de Nazaré	PI	collector	-42.2878	-4.6175
Rio Grande do Piauí	PI	collector	-43.1701	-7.7385
Vista Serrana	PB	collector	-37.5863	-6.6830
Cordeiros	BA	collection data	-41.9786	-15.1523
Imbassaí	BA	collector	-37.9592	-12.4785
Costa Azul	BA	collector	-37.5045	-11.6969
Subaúma	BA	collector	-37.7931	-12.2214
Antonina do Norte	CE	collector	-40.0441	-6.8184
Aracati	CE	collector	-37.7988	-4.5439
Boa Viagem	CE	collector	-39.6944	-5.2673
Camocim	CE	collector	-40.8575	-2.8686
Canindé	CE	collector	-39.3135	-4.6205
Iguatu	CE	collector	-39.0650	-6.4135
Itapipoca	CE	collector	-39.5675	-3.4886
Pedra Branca	CE	collector	-39.7074	-5.3367
Quixadá	CE	collector	-38.9415	-4.9587
Várzea da Conceição	CE	collector	-39.1102	-6.4735
Cajazeiras	PB	collector	-38.6255	-6.8825
Patos	PB	collection data	-37.3083	-7.0523
Arco Verde	PE	collector	-36.9441	-8.4043
Betânia	CE	Borges-Nojosa <i>et al.</i> 2005	-38.1982	-8.3087
Luís Côrrea	PI	collector	-41.6449	-2.8671
Monte Alegre de Sergipe	SE	collector	-37.5805	-9.9756
Currais Novos	RN	collector	-36.3832	-6.1994

Localities	State	Data source	Long	Lat
Natal	RN	collector	-35.2014	-5.8411
Santa Cruz	RN	collector	-36.0369	-6.1996

National Forest (FLONA), Ecological Station (EE), National Park (PARNA).

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Table S4. Climate and environmental values for each locality used to test genetic diversity in *Cnemidophorus ocellifer* through linear regression or simultaneous autoregression analyses. Nucleotide diversity ( $\pi$ ); niche suitability from current and Last Glacial Maximum (LGM, 21 kyr) periods; isothermality (Bio3), temperature seasonality (Bio4), minimum temperature of coldest month (Bio6), annual mean temperature (Bio1), annual precipitation (Bio12), net primary productivity (NPP), actual evapotranspiration (AET), topographic complexity (TC), and distance from center of origin (DCO). Letters after Bio3, Bio4 and Bio6 variables represent current (C) and LGM (L) climate conditions. Available at <http://costagc.weebly.com/publications.html>.

Table S5. Linear regression results that confirm the positive and significant association between Ecological Niche Modelling of *Cnemidophorus ocellifer* and the three most important current (C) climate variables to the model: isothermality (Bio3), temperature seasonality (Bio4), and minimum temperature of coldest month (Bio6).

<b>Variable</b>	<b>Std. Coeff.</b>	<b>VIF</b>	<b>t</b>	<b>P</b>
Bio3C	0.410	3.165	1.954	0.057
Bio4C	0.835	4.622	3.296	0.002
Bio6C	0.906	2.031	5.392	<0.001

Variance inflation factor (VIF), t-statistic (t), and P-value (P).



Table S6. Matrix of pairwise Euclidian distances for the 46 sampled localities of *Cnemidophorus ocellifer*. Available at <http://costage.weebly.com/publications.html>.

Table S7. Matrix of pairwise connectivity distance for the 46 sampled localities of *Cnemidophorus ocellifer* based on its current niche suitability. Available at <http://costagc.weebly.com/publications.html>.

Table S8. Matrix of pairwise connectivity distance for the 46 sampled localities of *Cnemidophorus ocellifer* based on its LGM niche suitability. Available at <http://costagc.weebly.com/publications.html>.

Table S9. Matrix of pairwise connectivity distance for the 46 sampled localities of *Cnemidophorus ocellifer* based on Caatinga main rivers. Available at <http://costagc.weebly.com/publications.html>.

Table S10. Matrix of pairwise resistance distance for the 46 sampled localities of *Cnemidophorus ocellifer* based on Caatinga slope gradient. Available at <http://costagc.weebly.com/publications.html>.

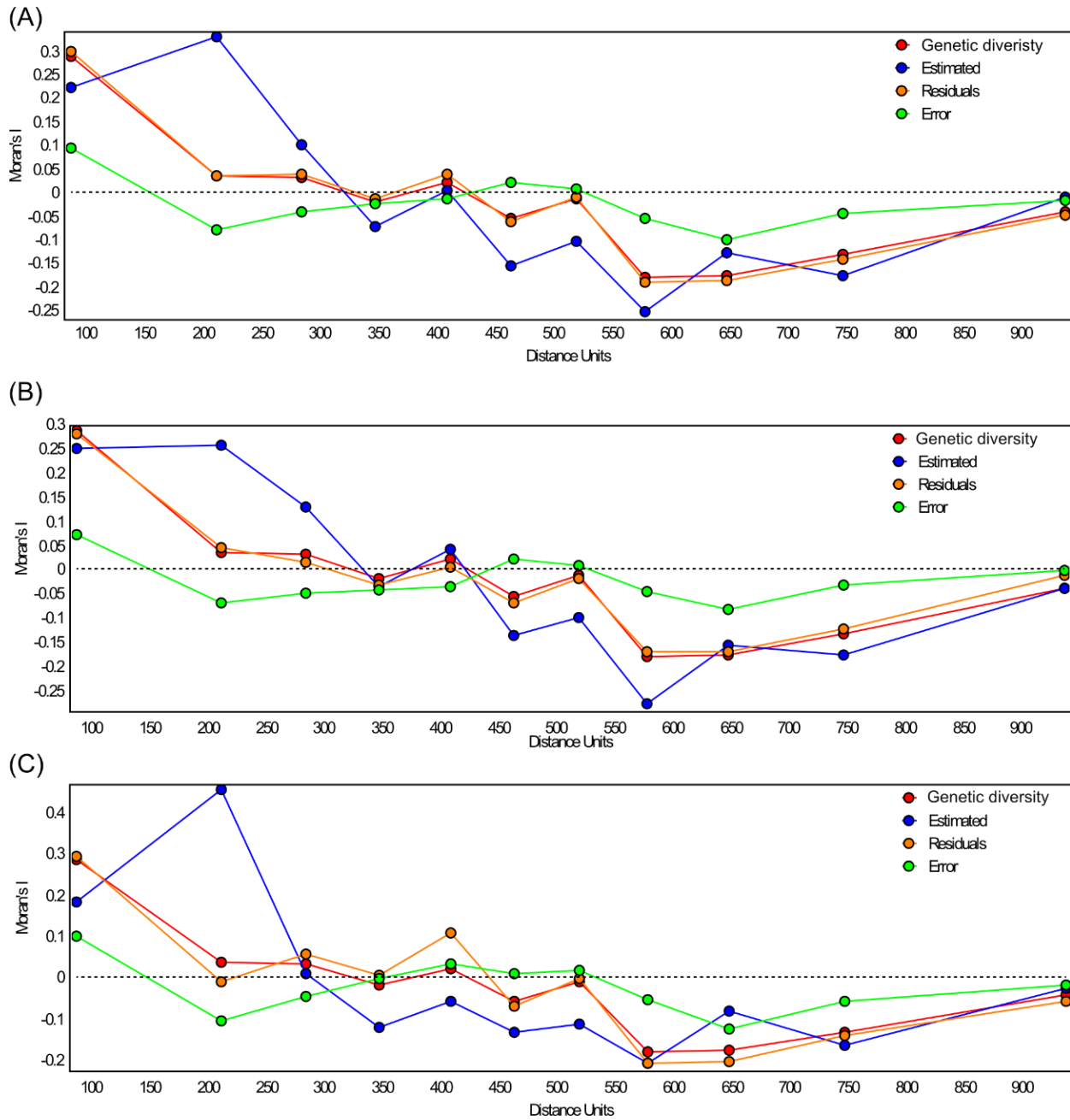
Table S11. Matrix of pairwise resistance distance for the 46 sampled localities of *Cnemidophorus ocellifer* based on Caatinga roughness gradient. Available at <http://costagc.weebly.com/publications.html>.

Table S12. Standardized coefficients of linear regressions that confirm the positive association between temperature variation and genetic diversity in *Cnemidophorus ocellifer*.

<b>Variable</b>	<b>Std. Coeff.</b>	<b>VIF</b>	<b>t</b>	<b>P</b>
Bio3L	0.755	1.717	4.636	<0.001
Bio4L	0.432	1.717	2.651	0.011
Bio3C	0.742	1.657	4.629	<0.001
Bio4C	0.422	1.657	2.631	0.012

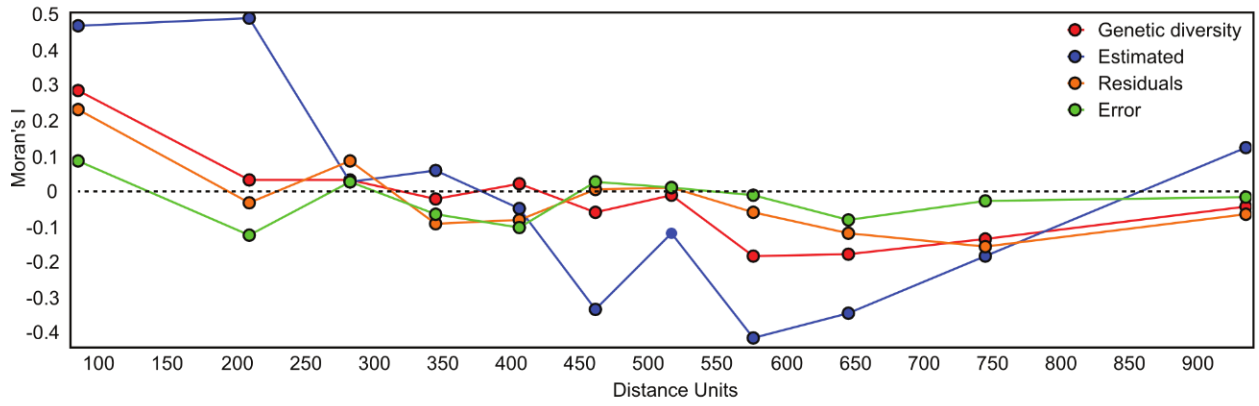
Isothermality (Bio3) and temperature seasonality (Bio4) in current (C) and LGM (L) conditions; variance inflation factor (VIF), t-statistic (t), and P-value (P).

Fig. S1. Correlograms of Moran's  $I$  coefficients calculated for 10 geographic distance classes (km) through simultaneous autoregression (SAR) between genetic diversity and (A) current niche suitability, (B) LGM niche suitability (C) refugia, (D) annual precipitation – Bio12, (E) topographic complexity, and (F) distance from center of origin. Spatial autocorrelation was absent at any distance in all models.

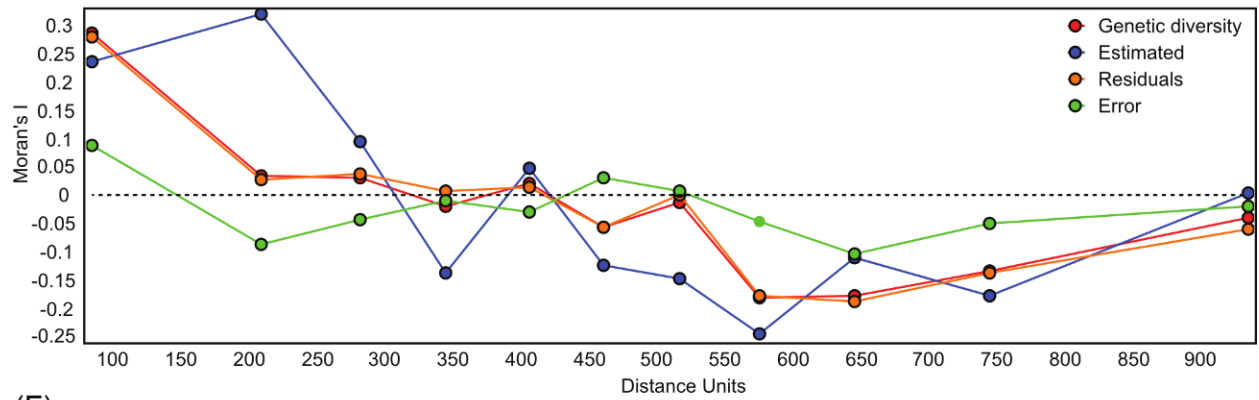




(D)



(E)



(F)

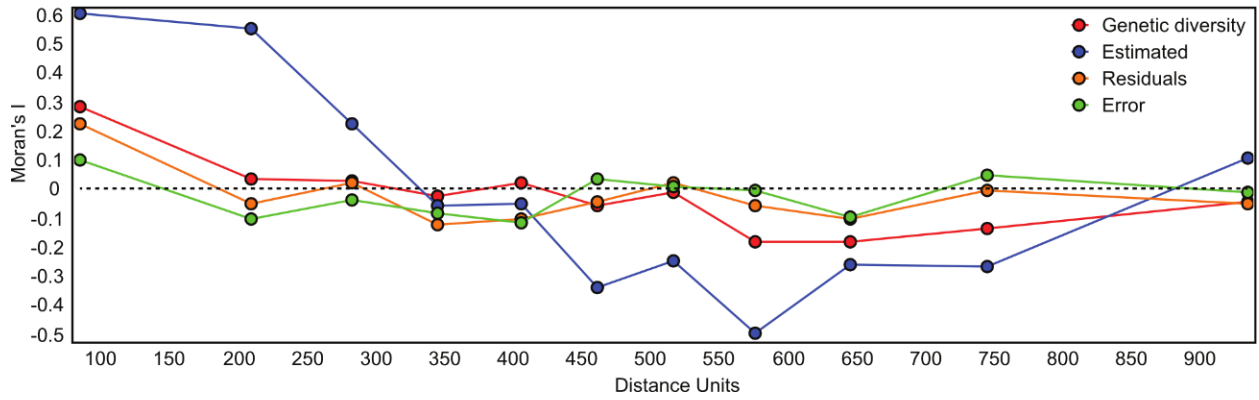


Fig. S2. Correlograms of Moran's  $I$  coefficients calculated for 10 geographic distance classes (km) through linear regressions between genetic diversity and (A) Bio3C+Bio4C, (B) Bio3L+Bio4C, and (C) Bio3L+Bio4L. Spatial autocorrelation was absent at any distance in both models.

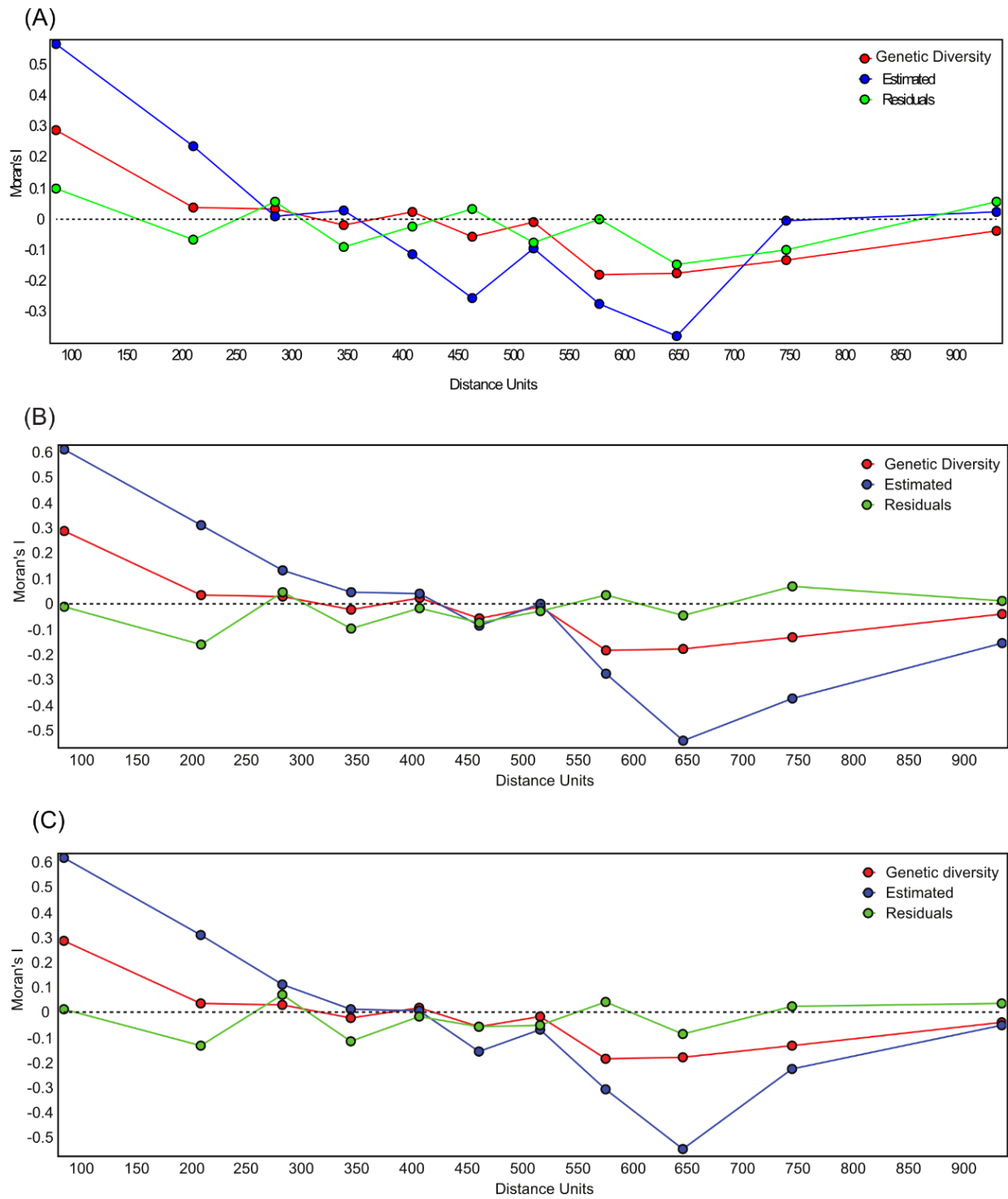


Fig. S3. Main rivers (A), slope (B) and roughness (C) rasters used in Circuitscape to generate the matrices of pairwise resistance distance to test genetic differentiation in *Cnemidophorus ocellifer*.

